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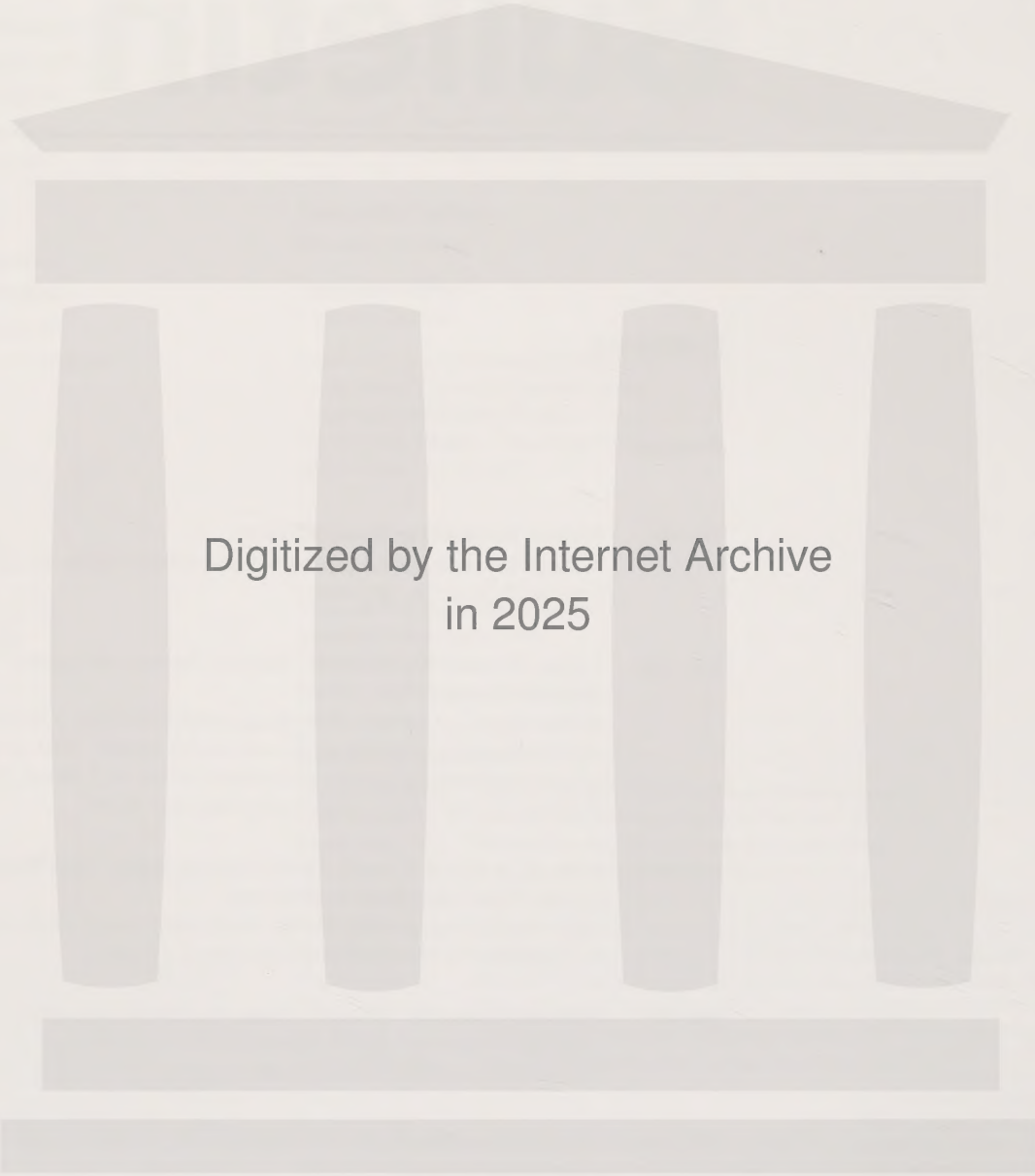
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Abstract—Stable isotope (SI) values of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) are useful for determining the trophic connectivity between species within an ecosystem, but interpretation of these data involves important assumptions about sources of intrapopulation variability. We compared intrapopulation variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for an estuarine omnivore, Spotted Seatrout (*Cynoscion nebulosus*), to test assumptions and assess the utility of SI analysis for delineation of the connectivity of this species with other species in estuarine food webs. Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values showed patterns of enrichment in fish caught from coastal to off-shore sites and as a function of fish size. Results for $\delta^{13}\text{C}$ were consistent in liver and muscle tissue, but liver $\delta^{15}\text{N}$ showed a negative bias when compared with muscle that increased with absolute $\delta^{15}\text{N}$ value. Natural variability in both isotopes was 5–10 times higher than that observed in laboratory populations, indicating that environmentally driven intrapopulation variability is detectable particularly after individual bias is removed through sample pooling. These results corroborate the utility of SI analysis for examination of the position of Spotted Seatrout in an estuarine food web. On the basis of these results, we conclude that interpretation of SI data in fishes should account for measurable and ecologically relevant intrapopulation variability for each species and system on a case by case basis.

Quantifying intrapopulation variability in stable isotope data for Spotted Seatrout (*Cynoscion nebulosus*)

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The mandate for management of fisheries has shifted toward a focus on ecosystem-based fisheries management (EFM) (Brodziak and Link, 2002). The EFM approach differs from historical single-species management in that EFM acknowledges the linkages between ecosystem components as well as the spatial and temporal variability in those linkages (Arkema et al., 2006; Christensen et al., 1996; NRC 1999; Thomas and Huke, 1996). The EFM paradigm has great potential to improve the ability of managers to accurately predict and appropriately respond to the impacts of multiple stressors on exploited fish populations. However, the data needs of EFM are high, and the acquisition of these data has generally lagged behind development of EFM theory (Dame and Christian, 2006).

Quantification of trophic connections among species is an important precursor for the shift to EFM because such data support the development of food-web network models that allow fishing pressure to be analyzed in an ecological context with other sources of mortality (Christensen and Pauly, 2004). Quantitative techniques, like stable isotope (SI) analysis, have been widely applied to fish populations as a method for quantification of the trophic links between predator and prey (Power et al., 2002; Rooker et al., 2006). Stable isotope data are well suited to

the development of network models of food webs because they are time-integrated and provide data on the relative importance of entire trophic pathways down to sources of primary production (Peterson and Fry, 1987). Yet, the interpretation of stable isotope data requires several important assumptions, and these assumptions should be carefully analyzed if results may affect management decision making.

Key assumptions made in interpreting stable isotope data involve the sources of variability in isotopic values for a given population (Peterson and Fry, 1987). Population variability integrates several sources of variability, including environmental influences (Barnes et al., 2008), differences in individual behavior (Sweeting et al., 2005), ontogeny, growth, and tissue turnover rates (Herzka, 2005; Perga and Gerdeaux, 2005), and prey availability and feeding success (Sweeting et al., 2005). Partitioning out these sources of variability, particularly for an omnivorous consumer in an estuarine ecosystem, can be complex. In particular, quantification of intrapopulation variability in isotope data (e.g., variability due to differences in individual behavior or tissue turnover rates) is important for separating this variability from changes that are ecologically important (e.g., changes due to ontogeny or the environment).

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Intrapopulation variability in SI compositions can be particularly difficult to interpret in species and ecosystems with multiple overlapping trophic pathways. Omnivorous fish species, such as Eurasian Perch (*Perca fluviatilis*) and Spotted Seatrout (*Cynoscion nebulosus*), hold important positions in aquatic food webs as trophic mediators of primary production, but they have complex stable isotope signatures that require a close examination of assumptions regarding intrapopulation variability (Quan et al., 2007; Quevedo et al., 2009). The estuarine habitat of Spotted Seatrout, in particular, is highly complex; it contains both potential aquatic sources (e.g., phytoplankton, microphytobenthos, submerged aquatic vegetation, marsh macrophytes) and terrestrial sources of primary production that can vary in importance for estuarine food webs, both temporally and spatially. One of the key questions with the food-web approach to EFM that can be addressed with stable isotope data is an estimation of the relative importance of different sources of organic matter for the production of estuarine consumers. Yet, individual fishes exposed to the same suite of prey resources may have very different isotopic values, and that variation may overemphasize the importance of omnivory and confound detection of any population-level differences in isotope ratios (Zanden et al., 2010). The utility of stable isotope data for analysis of estuarine ecosystems will be greatly enhanced when sources of uncertainty have been well-quantified for important populations.

The goal of this analysis was to measure intrapopulation variability in carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) SI values in a representative estuarine omnivore (Spotted Seatrout) to improve understanding and interpretation of SI data in an estuarine ecosystem in the northern Gulf of Mexico. The study objectives were 1) to quantify individual variation in carbon and nitrogen isotopic values of Spotted Seatrout in the laboratory and in wild populations; 2) to examine spatial and seasonal changes in the isotopic value of various tissue types with different turnover rates; and 3) to quantify intrapopulation variability for carbon and nitrogen isotopes in the laboratory and compare these estimates with field-based and literature reported values for isotope variability. A characterization of these sources of variability will allow for a clearer interpretation of how opportunistic changes in fish diet may be reflected in seasonal or spatial variances in isotope values.

Methods

Spotted Seatrout were collected from regular surveys conducted monthly by the University of Southern Mississippi Center for Fisheries Research and Development at 8 sites in coastal Mississippi (Fig. 1). Additional fish were also captured at 2 additional sites as part of a second survey of composition of fish communities associated with oyster reefs in the western Mississippi Sound (Fig. 1). Both surveys were conducted from 2007

to 2009. All fish were captured during 1-h sets of an experimental gillnet with 5 panels (30.48×1.83 m with mesh sizes of 50.8, 63.5, 76.2, 88.9, and 101.6 mm). All Spotted Seatrout collected were identified based on taxonomic descriptions of Hoese and Moore (1977), measured to the nearest 1 mm (total length [TL]) and weighed to the nearest 1 g (wet weight), returned to the laboratory on ice, and immediately frozen at -20°C . In the laboratory, fish were thawed and tissue samples were collected: 2 samples of white muscle were collected from the left and right side of the fish dorsal to the midline, and 2 samples were collected of liver tissue. Both muscle and liver samples were freeze-dried to a constant weight, ground to a fine power, homogenized, and stored in a desiccator for stable isotope analysis.

Stable isotope ratios for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were employed to delineate spatial and temporal changes in the SI values of individual fish within and between local populations. The high lipid content of liver tissue necessitated the need for a correction factor because lipids are typically depleted in ^{13}C relative to carbohydrates and protein (Deniro and Epstein, 1977). Ten liver samples were split into 2 parts; lipid was extracted from half the sample and the other half was unaltered. Each lipid subset of liver tissue samples was extracted sequentially with 2:1 chloroform:methanol and 1:2 chloroform:methanol mixtures, dried, and homogenized before analysis (Bligh and Dyer, 1959; Ruiz et al., 2007). The $\delta^{13}\text{C}$ results of the lipid-extracted samples were plotted against the results of the nonextracted samples, and the resultant linear equation was used to correct the liver $\delta^{13}\text{C}$ values for lipid content:

$$\delta^{13}\text{C}_{\text{extracted}} = (0.9975 \times \delta^{13}\text{C}_{\text{nonextracted}}) + 2.0578, (1)$$

where the coefficient of determination [r^2] = 0.93.

Samples were analyzed with a DELTA V Advantage¹ stable isotope ratio mass spectrometer (Thermo Scientific, Waltham, MA) coupled to an ECS 4010 elemental combustion system (Costech Analytical Technologies, Inc., Valencia, CA). All samples were analyzed in duplicate and referenced to known isotopic standards and are reported in per mil notation (‰). Nitrogen is referenced to atmospheric nitrogen and carbon to the Pee Dee Belemnite (PDB) standard.

The $\delta^{15}\text{N}$ value was used to calculate mean trophic level by site and month based on a general formula reported by Rooker et al. (2006):

$$\text{Trophic level} = 1.0 + (\delta^{15}\text{N} - 6.0)/3.2, (2)$$

where 3.2 is the reported mean fractionation factor for nitrogen in fish (Peterson and Fry, 1987; Post, 2002) and 6.0 is the mean $\delta^{15}\text{N}$ value of primary producers in Gulf of Mexico coastal estuaries on the basis of both analysis of samples collected as part of separate projects in Mississippi Sound (senior author, unpubl. data)

¹ Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

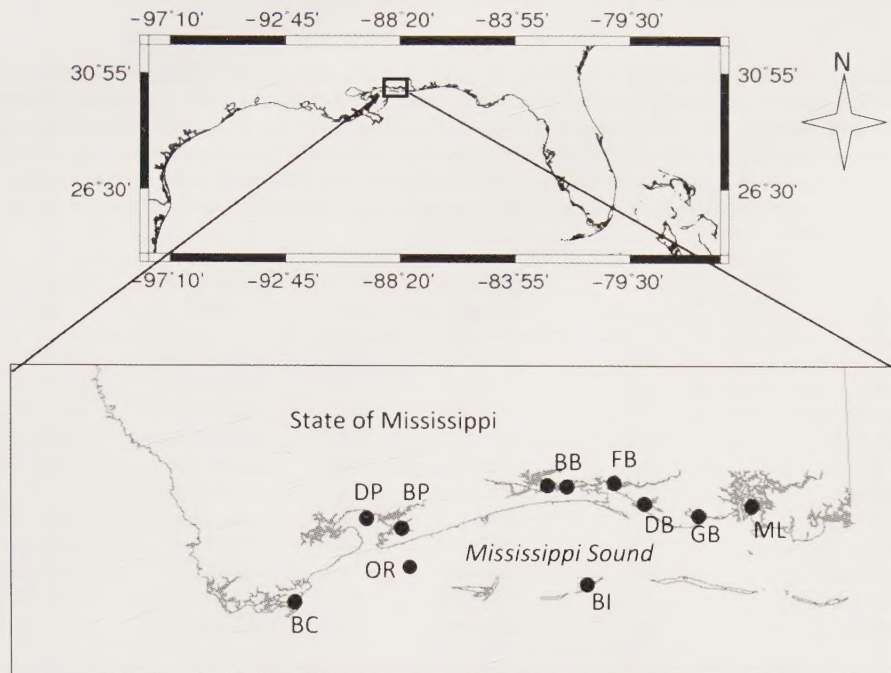


Figure 1

Map of 10 collection sites for Spotted Seatrout (*Cynoscion nebulosus*) captured in coastal Mississippi and the western Mississippi Sound during 2007–09 for this study of intrapopulation variability in stable isotope values for this species. Sites are labeled as Bayou Caddy (BC), Dupont (DP), Bayou Portage (BP), oyster reefs (OR), Back Bay (BB, 2 locations), Fort Bayou (FB), Davis Bayou (DB), Graveline Bayou (GB), Marsh Lake (ML), and Barrier Islands (BI). Fish were collected at random at the Barrier Island site, and therefore fish collected at the Barrier Islands may have been collected adjacent to either of the 2 largest of the Barrier Islands.

and similar values reported in the literature for the coastal Gulf of Mexico (Winemiller et al., 2007). Previously reported $\delta^{15}\text{N}$ values for primary producers—needlegrass rush (*Juncus roemerianus* Scheele), smooth cordgrass (*Spartina alterniflora*), and edaphic algae—in a salt marsh within Graveline Bayou ranged from 5.2‰ to 6.1‰ (Sullivan and Moncreiff, 1990). Values for shoalweed (*Halodule wrightii* Asch.), associated epiphytes, and sand microflora from Horn Island were reported to range from 4.4‰ to 7.8‰, and various species of macroalgae from the same site had $\delta^{15}\text{N}$ values ranging from 4.7‰ to 10.0‰ (Moncreiff and Sullivan, 2001). Although much remains to be learned about nitrogen sources and variability within Mississippi Sound as one travels from the mainland to the Barrier islands, the average $\delta^{15}\text{N}$ value of 6.0 was considered a reasonable estimate on the basis of the data available. Intrapopulation variability of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was calculated separately on the basis of a comparison of isotope ratios for hatchery-reared Spotted Seatrout ($n=20$) fed with a single processed food. Fish used for variability estimates were kept under constant conditions of temperature and salinity and fed continually from a fixed food source for at least 6 months before analysis. This

food source was a commercially available pellet food used successfully in the culture of Spotted Seatrout (Blaylock²), and all feed used for this study was taken from a single lot to assure compositional consistency.

Stable isotope data were analyzed to quantify differences in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values by location and sampling month with an analysis of variance (ANOVA). All post-hoc comparisons were conducted with a Tukey's honestly significant difference (HSD) test. The relationships between both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values and fish size also were fitted to a simple linear regression to test for the existence of a slope significantly greater than zero that would indicate a relationship between isotope enrichment and fish size. Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes values in liver tissue were compared with results from white muscle and tested for deviation from a 1:1 relationship with a comparison of slopes (t -test). All statistical tests were conducted with a type-I error rate of 0.05.

² Blaylock, R. 2011. Personal commun. Thad Cochran Marine Aquaculture Center, Gulf Coast Research Laboratory, Univ. Southern Mississippi, 703 East Beach Road, Ocean Springs, MS 39564.

Table 1

Summary of mean total length (TL, mm), sample size (n), and mean carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope values (‰) and their standard deviations (SD) by sample location for Spotted Seatrout (*Cynoscion nebulosus*) collected at 10 sites in coastal Mississippi and the western Mississippi Sound in 2007–09. Data for “reference” samples were obtained from laboratory-reared fish used to calculate intrinsic variability. Map code refers to site labels in Figure 1. The map code *na* (not available) indicates that the reference fish are not shown in Figure 1.

Location	Map code	TL [mm] (SD)	n	Mean $\delta^{13}\text{C}$ (SD)	Mean $\delta^{15}\text{N}$ (SD)
Bayou Caddy	BC	323(61)	30	-20.8(0.9)	14.3(0.9)
Dupont	DP	289(54)	9	-21.9(1.8)	13.7(1.2)
Bayou Portage	BP	279(45)	31	-22.6(1.3)	13.5(0.8)
Oyster reefs	OR	357(51)	24	-21.7(1.1)	14.3(0.6)
Back Bay	BB	366(53)	10	-22.1(1.9)	14.8(0.6)
Fort Bayou	FB	290(54)	4	-21.0(1.3)	14.7(1.0)
Davis Bayou	DB	296(71)	16	-21.3(1.4)	13.1(1.1)
Graveline Bayou	GB	271(47)	15	-20.6(1.1)	12.8(0.8)
Marsh Lake	ML	439(40)	2	-20.6(1.4)	14.4(0.6)
Barrier Islands	BI	500(76)	33	-19.1(1.7)	15.1(1.0)
Reference	na	210(13)	20	-18.03(0.24)	12.74(0.2)

Finally, to assess the potential bias on sample variability with pooling fish for analysis of $\delta^{13}\text{C}$ isotope values, a simple resampling numerical experiment was conducted on data from all site and date combinations that produced at least 30 fish for analysis. Subsamples that consisted of between 2 and 20 randomly selected fish were averaged to produce a “pooled” value for $\delta^{13}\text{C}$, and means of pooled data were calculated from each pooled subsample ($n=10$ subsamples selected with replacement) for each resampled size. These data were then plotted to assess bias in the result by comparison of the resampled mean with the nonpooled sample mean for each set of data. The pattern in the absolute residuals was examined as a function of resample size to estimate minimum effective pooled sample size for each data set.

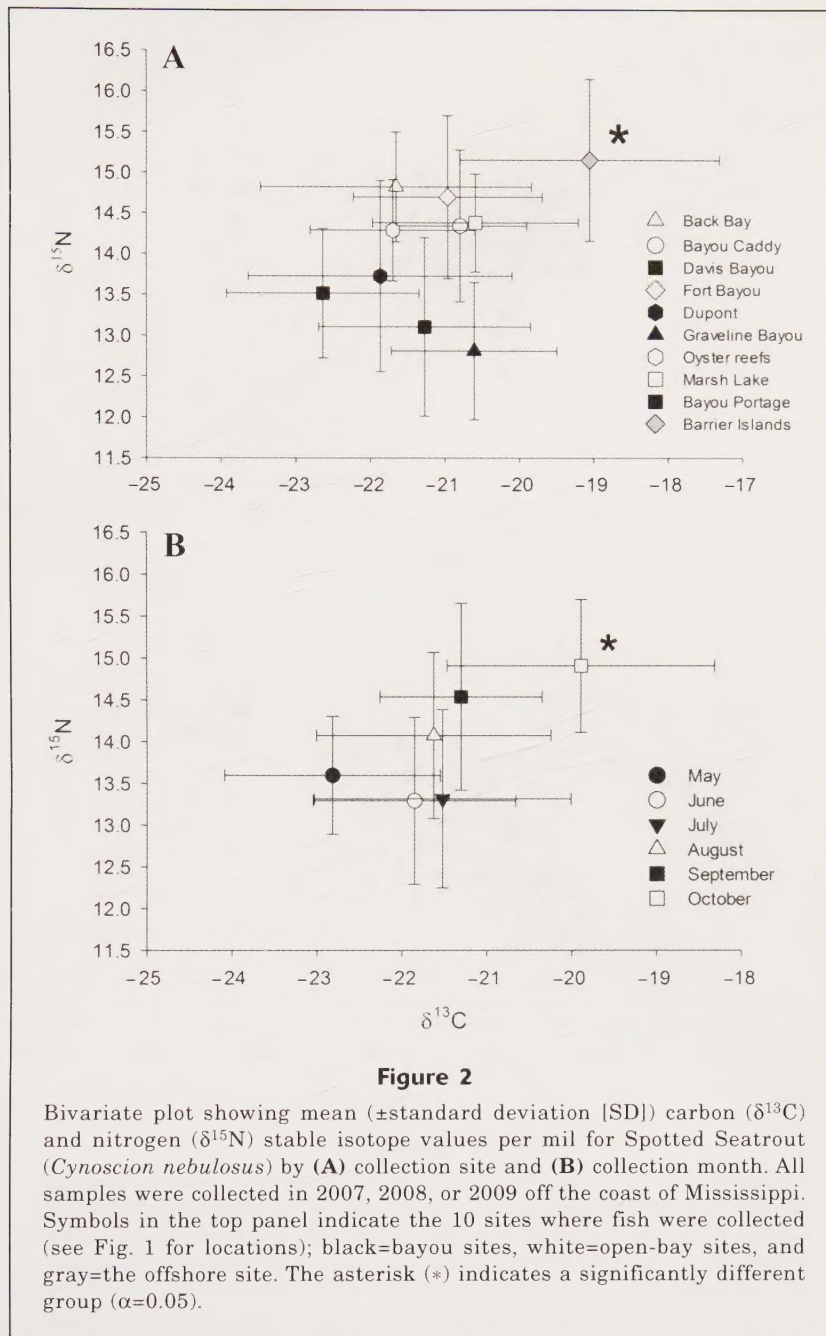
Results

From 10 sites over the period of 2007–09, 187 individual Spotted Seatrout were captured (Fig. 1, Table 1). All fish were captured between May and October and sampling coverage was relatively even across months with the exception of September, which yielded only 3 fish. Fish ranged in size from 212 to 622 mm TL, but mean TL by site was 250–350 mm TL with the exception of fish collected near the Barrier Islands. The mean $\delta^{13}\text{C}$ for all fish across all sites was -21.4‰ (standard deviation [SD] of 1.6‰ .) The system-wide standard deviation was generally similar to the within-site standard deviation but close to the within-site maximum (Table 1). The mean $\delta^{15}\text{N}$ across all sites was 13.9‰ (SD of 1.1‰ .) As with $\delta^{13}\text{C}$, the overall standard deviation was

within the range of within-site variability but toward the high end of the range. On the basis of the $\delta^{15}\text{N}$ data, Spotted Seatrout collected from field sites feed at a mean trophic level of 3.4. The standard deviation of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for reference fish raised in the laboratory was $<20\%$ of field-based estimates of within-sample variability (Table 1).

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope ratios of Spotted Seatrout showed an inshore-to-offshore and summer-to-fall enrichment trend. Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values examined showed a statistically significant trend across sites ($\delta^{13}\text{C}$ ANOVA, $F_{9,161}=2.61$, $P=0.008$; $\delta^{15}\text{N}$ $F_{9,161}=3.44$, $P<0.0001$) and sample months ($\delta^{13}\text{C}$ ANOVA, $F_{5,161}=7.35$, $P<0.0001$; $\delta^{15}\text{N}$ $F_{5,161}=9.29$, $P<0.0001$). Post-hoc analysis indicated a significant difference between fish collected at inland, marsh-associated sites, such as Graveline Bayou, Davis Bayou, Bayou Portage, and Dupont, and fish captured near the Barrier Islands (Fig. 2A). Isotope values overlapped considerably among more open-water sites in Mississippi Sound (Bayou Caddy and oyster reefs), Marsh Lake, and Back Bay at both marsh-associated sites and Barrier Islands sites, but the open-water sites were closer than the Barrier Islands sites in isotopic value to marsh-associated sites. In terms of months, June, July, and August were statistically different from October, but this difference was confounded with site differences because most fish captured in October were from around the Barrier Islands (Fig. 2B). There was also a small but significant positive linear trend in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with fish TL (Fig. 3).

The lipid-corrected stable isotope values of Spotted Seatrout liver samples were similar to results from white muscle for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ but contained no-



ticeable bias. The relationship between lipid-corrected $\delta^{13}\text{C}$ data from liver samples and data for muscle displayed a relationship significantly different from 1:1 (t -test, slope=0.25, $P<0.001$; Fig. 4A) with a shift from positive to negative bias in liver $\delta^{13}\text{C}$ values as muscle $\delta^{13}\text{C}$ values increased. However, although $\delta^{15}\text{N}$ values also showed a linear trend between liver and muscle samples with a slope that differed significantly from one ($\delta^{15}\text{N}$ slope=0.50, $P<0.001$), liver tissue showed more consistent depletion bias than muscle tissue (Fig. 4B). This bias increased with overall enrichment of $\delta^{15}\text{N}$ in muscle tissue.

The resampling procedure was performed on data from 3 sites: Bayou Portage, Bayou Caddy, and the Barrier Islands. These sites had the largest sample sizes and showed some contrast between nearshore and open-water sites. Intersample variability was related to pooled resample size (n ; Fig. 5). A high mean absolute residual value (>0.1) was observed for $n\leq 3$ but dropped rapidly to a value <0.05 for an $n>5$. This pattern was consistent across sites despite a large difference in residual values at smaller pooled resample sizes. In general, bias in mean isotopic ratio was minimal at any pooled resample size greater than $n=5$.

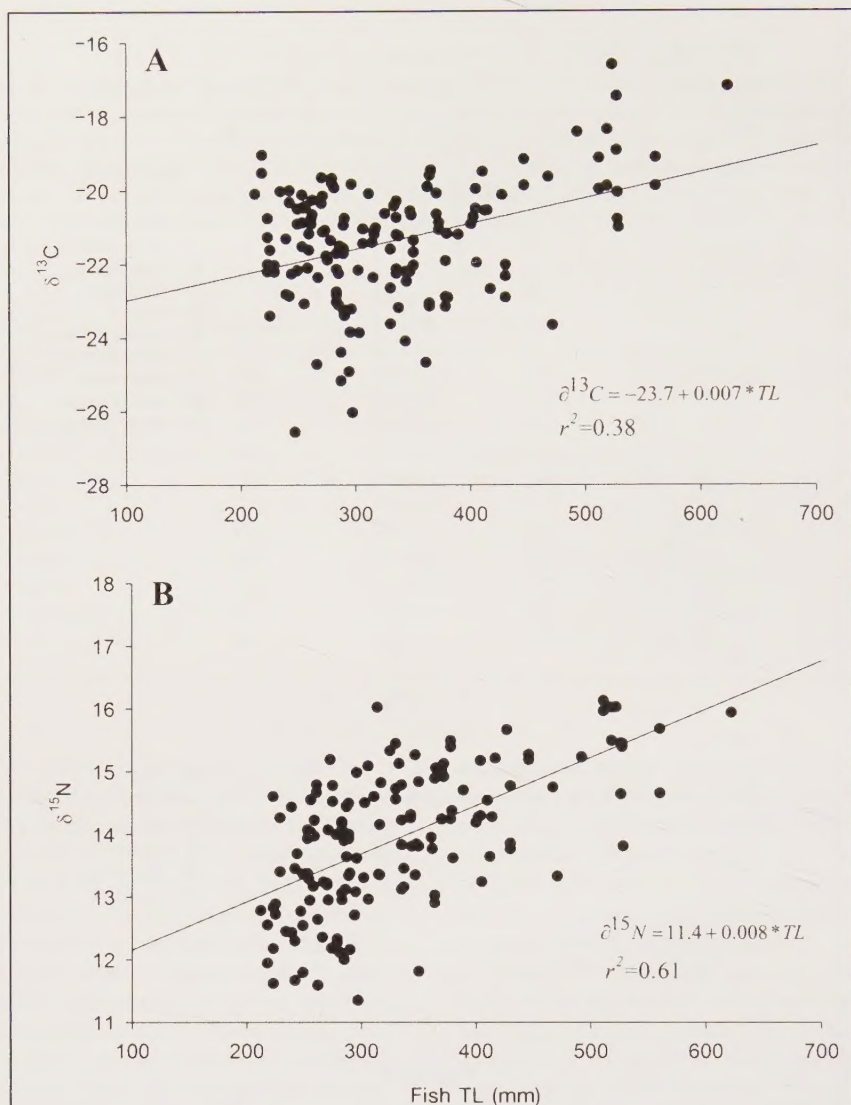


Figure 3

Scatter plot of fish total length (TL, mm) against (A) carbon ($\delta^{13}\text{C}$) and (B) nitrogen ($\delta^{15}\text{N}$) stable isotope values per mil for Spotted Seatrout (*Cynoscion nebulosus*) examined in this study. The solid line on each panel indicates the best-fit regression line for each data set. r^2 =coefficient of determination.

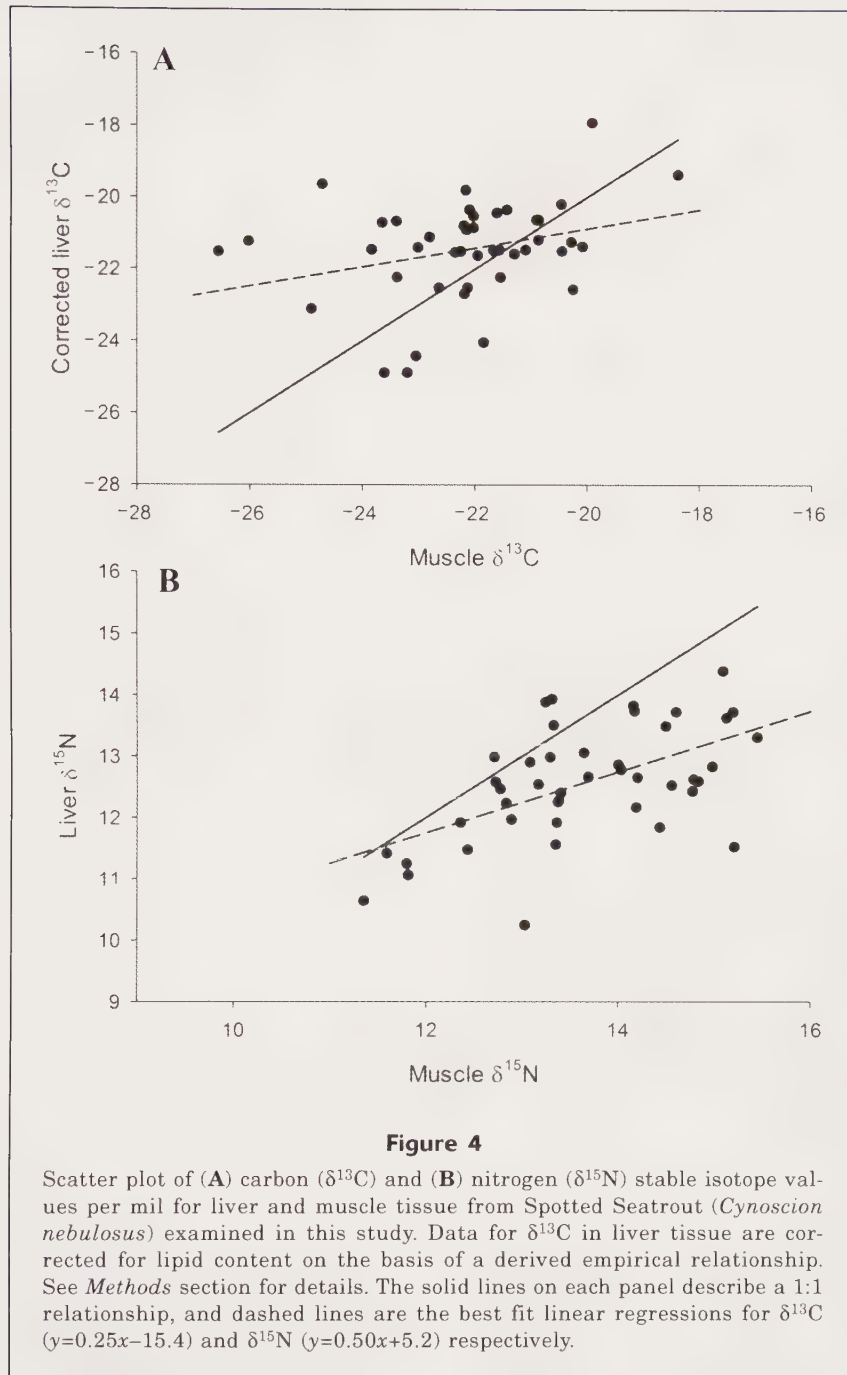
Discussion

Effects of tissue type, fractionation, and fish size

Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ SI values can differ between tissue types (Pinnegar and Polunin, 1999). Differences between the isotopic values of fish liver and muscle tissue have been ascribed to differences in tissue turnover rates of liver and muscle (Sweeting et al., 2005), and to seasonal differences in growth rates, feeding behavior, and prey availability (Perga and Gerdeaux, 2005). However, in subtropical waters, such as Missis-

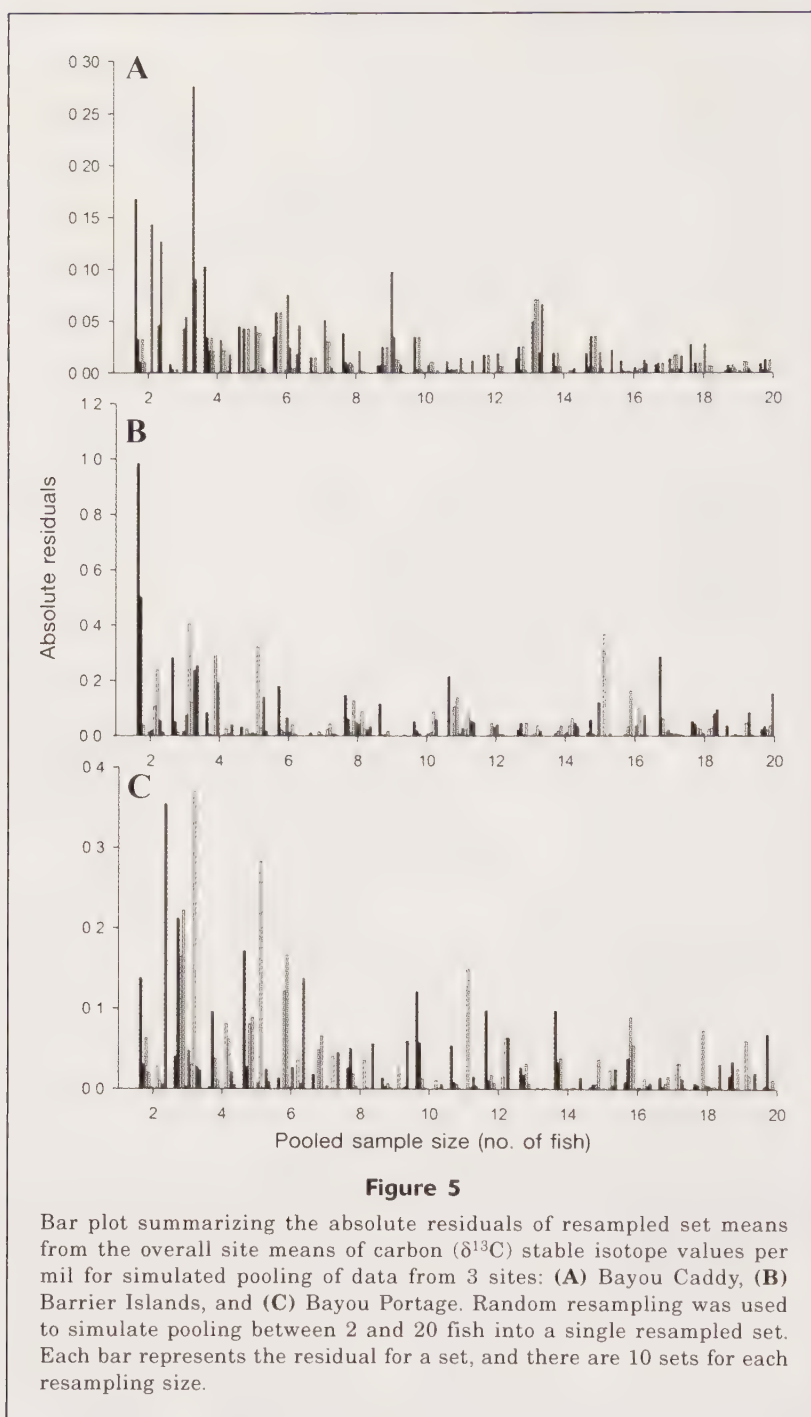
sippi Sound, fish growth likely occurs throughout the year (Vetter, 1982), and, in this study, $\delta^{13}\text{C}$ values of liver and muscle were generally very similar, indicating that the pattern reported by Perga and Gerdeaux (2005) at more northern latitudes was not observed in this study. The isotopic values for $\delta^{15}\text{N}$ did show a negative bias in liver compared with muscle. Because all sampling occurred during periods of probable high growth (summer and fall), this result may be related to differences in isotopic fractionation and turnover rates between tissue types.

The increase in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with fish size



was small but significant and generally supports an increase in trophic level as fish grow and move offshore. The increase in $\delta^{15}\text{N}$ observed over the size range of fish in our study was close to 3‰, nearly a full trophic level. The size range of fish in this study was relatively wide but probably includes only fish beyond their first year—an assumption made on the basis of published growth curves (Fulford and Hendon, 2010). The probable age range of these fish suggests that an ontogenetic diet shift associated with maturation is dif-

ficult to extrapolate from these data because the trend of increasing heavy isotope values is confounded by changes in prey availability, by increases in fish prey capture efficiency with seatrout size, and by the potential variability of carbon and nitrogen sources within the Mississippi Sound and its subestuaries. The largest Spotted Seatrout were caught in open water, mainly offshore near the Barrier Islands, where prey fishes of higher trophic level, such as anchovies (e.g., Striped Anchovy [*Anchoa hepsetus*]) that have a mean trophic



level similar to that of Spotted Seatrout captured at inshore sites, may be more prevalent.

Spatial and temporal differences in SI

Spatial and temporal patterns in SI composition were interrelated and consistent with a seasonal offshore movement of individual fish (Hendon et al., 2002). Overall, across all sites, mean $\delta^{13}\text{C}$ for Spotted Seatrout

in coastal Mississippi suggests a stronger influence of pelagic primary production than of terrestrial sources on the diet of Spotted Seatrout. Yet, there was a detectable trend: the least-enriched samples were collected in nearshore waters in small embayments, and the most-enriched samples were collected farther offshore near the Barrier Islands. A clear inshore-to-offshore pattern of enrichments was also displayed by $\delta^{15}\text{N}$ SI values, a finding that is consistent with increases in trophic

level as fish begin to migrate offshore, although spatial variability in $\delta^{15}\text{N}$ may also contribute to the observed differences. There was much overlap between sites, but the separation of small embayments from the Barrier Islands was detectable in both carbon and nitrogen, and therefore the seasonal–spatial pattern seems robust for within-site variability and occurs at a temporal scale larger than that for the tissue isotopic turnover rate.

These results also are consistent with isotopic values of Spotted Seatrout in Graveline Bayou reported by Sullivan and Moncreiff (1990), who found that Spotted Seatrout had a mean $\delta^{13}\text{C}$ value of -20.7 and a mean $\delta^{15}\text{N}$ ratio of 11.8 —results that are very similar to the values reported here for Spotted Seatrout caught in Graveline Bayou. Our data, however, also indicate that these values are the middle of the overall range for $\delta^{13}\text{C}$ and near the bottom of the range for $\delta^{15}\text{N}$ across all sites in Mississippi. A more comprehensive analysis of Spotted Seatrout position in the coastal food web will require sampling over a broad spatial and temporal scale. Still, ecological patterns, such as spatial and temporal differences in SI values, are detectable, and therefore stable isotope data can be used for understanding trophic relationships in this species.

Individual variability in SI composition within a population can confound ecological patterns particularly for omnivores (Quevedo et al., 2009; Sweeting et al., 2005). Population variability can be caused by individual physiological differences (i.e., differences in isotopic fractionation or growth and tissue turnover rates); individual differences in behavior, prey availability or prey preference; and changes in environmental conditions that may influence individual movement, metabolism, growth, and diet (Barnes et al., 2008). Our analysis shows that individual variability measured in the laboratory with a diet of a single commercial feed is quite low (standard deviation = 0.24) in comparison with that derived from field studies (median standard deviation = 1.5), showing that ecologically relevant isotopic variability in Spotted Seatrout is detectable in field populations.

Detection of population-level differences through space and time can be confounded by this individual variability within population-level samples. Pooling of individuals into a common sample for analysis is, therefore, an often used method for reduction of individual variability to increase the focus on population-level questions. How much pooling is enough to reduce individual variation? Our resampling experiment indicates that the effectiveness of pooling is maximized for a subsample size of 5–6 individual fish. Smaller subsamples introduced potential bias due to individual variation, and larger subsamples reduced sampling efficiency. In general, we advocate pooling only for investigations of interpopulation differences or for changes in a single population through time. Individual variability has been found to be important in detection of behavior patterns (Sweeting et al., 2005) and in com-

munity-level studies (Bolnick et al., 2003; Matthews and Mazumder, 2004).

Conclusions

Understanding the trophic role of omnivores, such as Spotted Seatrout, is a critical part of estuarine ecosystem-based management, and SI analysis is a valuable tool for trophic studies of this species. Diet data are needed for identification of important prey species, but such data can be biased by small sample sizes and do not provide information on differences in total assimilation across prey species. Stable isotope analysis is an important complementary tool that allows the characterization of trophic pathways at broader spatial and temporal scales. However, variability in SI values within a population can be caused by factors unrelated to diet shifts, and these mitigating factors must be accounted for and incorporated into trophic studies to achieve meaningful results.

Our findings substantiate the utility of stable isotope analysis for quantification of the trophic role of Spotted Seatrout in an estuarine system and demonstrate that this trophic role changes spatially and temporally in predictable ways that can be incorporated into ecosystem studies. The trophic role of Spotted Seatrout is not static, it is dependent on factors, such as habitat, life stage, and fish size that are not independent of one another. Spotted Seatrout are known to display minimal movement before sexual maturation (Hendon et al., 2002), and this behavior indicates that the observed patterns in trophic role are related more to alterations in migration patterns as fish grow rather than to opportunistic movement not related to ontogeny. Such distinctions are important for understanding the role of a fish population within an ecosystem, and this research will directly benefit the more comprehensive study that is needed to understand the impact of habitat on Spotted Seatrout production. More broadly, patterns in both intra- and interpopulation variability in SI values need to be well understood for SI analysis to provide an unbiased measure of trophic connectivity within estuarine ecosystems. Studies such as this one that explicitly measure these variables in a target ecosystem are extremely valuable for the application of SI data to ecosystem management.

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Abstract—Western Atlantic synodontid species were studied as part of an ongoing effort to reanalyze Caribbean shorefish diversity. A neighbor-joining tree constructed from cytochrome *c* oxidase I (COI) data revealed 2 highly divergent genetic lineages within both *Synodus intermedius* (Agassiz, 1829) (Sand Diver) and *S. foetens* (Linnaeus, 1766) (Inshore Lizardfish). A new species, *Synodus macrostigmus*, is described for one of the *S. intermedius* lineages. *Synodus macrostigmus* and *S. intermedius* differ in number of lateral-line scales, caudal pigmentation, size of the scapular blotch, and shape of the anterior-nostril flap. *Synodus macrostigmus* and *S. intermedius* have overlapping geographic and depth distributions, but *S. macrostigmus* generally inhabits deeper water (>28 m) than does *S. intermedius* and is known only from coastal waters of the southeastern United States and the Gulf of Mexico, in contrast to those areas and the Caribbean for *S. intermedius*. *Synodus bondi* Fowler, 1939, is resurrected from the synonymy of *S. foetens* for one of the *S. foetens* genetic lineages. The 2 species differ in length and shape of the snout, number of anal-fin rays, and shape of the anterior-nostril flap. *Synodus bondi* and *S. foetens* co-occur in the central Caribbean, but *S. bondi* otherwise has a more southerly distribution than does *S. foetens*. Redescriptions are provided for *S. intermedius*, *S. foetens*, and *S. bondi*. Neotypes are designated for *S. intermedius* and *S. foetens*. A revised key to *Synodus* species in the western Atlantic is presented.

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A new species of western Atlantic lizardfish (Teleostei: Synodontidae: *Synodus*) and resurrection of *Synodus bondi* Fowler, 1939, as a valid species from the Caribbean with redescrptions of *S. bondi*, *S. foetens* (Linnaeus, 1766), and *S. intermedius* (Agassiz, 1829)

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The aulopiform lizardfish family Synodontidae is represented in the western Atlantic by 3 genera: *Synodus* (5 species recognized before this study), *Saurida* (4), and *Trachinocephalus* (1). Lizardfishes are benthic predators in numerous ecosystems, including coral reefs, estuaries, and reef structure or sandy bottom areas on continental shelves (Anderson et al., 1966; Cressey, 1981; Randall, 2009). Once thought to occupy a mid-trophic position and employ a sit-and-wait predation strategy, adult lizardfishes now are known to occupy a high trophic position—apex in some systems—as active hunters feeding primarily on other predatory fishes (Cruz-Escalona et al., 2005).

Despite having no commercial value as food fishes, *Synodus* spp. and *Saurida brasiliensis* (Largescale Lizardfish) are caught as bycatch in shrimp-trawl fisheries in the western Atlantic, accounting for 1.5% and 1.8% of total-catch biomass in the Gulf of Mexico and North Carolina,¹

respectively (Jeffers et al., 2008; Manjarrés et al., 2008). Populations of *Synodus foetens* (Linnaeus, 1766) (Inshore Lizardfish) are estimated to be at fully exploited levels as bycatch in Gulf of Mexico shrimp-trawl fisheries (Garcia-Abad et al., 1999; Wells, 2007; Jeffers et al., 2008). Proper management and ecological investigation of commercially fished species require an accurate understanding of species diversity. For example, Collette et al. (1978) discovered that the Caribbean and Brazilian populations of the commercially important *Scomberomorus maculatus* (Spanish Mackerel) constitute a distinct species, which they named *S. brasiliensis* (Serra). Without this systematic study, populations of *S. brasiliensis* would still be managed under the same plan as *S. maculatus*.

for North Carolina. Job 3: characterization of the near-shore commercial shrimp trawl fishery from Carteret County to Brunswick County, North Carolina. Southeast Fisheries Science Center, Miami, FL, 29 p. [Available online from <http://www.sefsc.noaa.gov/sedar/download/SEDAR20-ASMFC-DW09.pdf?id=DOCUMENT>]

¹ Brown, K. 2009. Interstate fisheries management program implementation

Scientists have periodically investigated the systematics of synodontids since Linnaeus (1758) described *Esox synodus* in the mid-18th century. Throughout the 19th century, researchers described 17 *Synodus* species in the western Atlantic (Anderson et al., 1966; Meek, 1884; Norman, 1935). In the most recent comprehensive treatments of western Atlantic lizardfishes (Anderson et al., 1966; Russell, 2003), 5 species of *Synodus* have been recognized. Ongoing research to evaluate diversity of the Caribbean ichthyofauna with DNA barcoding (Hebert et al., 2003) and traditional morphological investigation have led to the recent discovery of many new cryptic fish species and the resurrection of several formerly synonymized ones in what were thought to be well-studied taxa (Baldwin and Weigt, 2012; Baldwin et al., 2009, 2011; Tornabene et al., 2010; Victor, 2007, 2010). In the course of the present work, discrepancies were revealed between barcode data and the currently accepted species classification of western Atlantic *Synodus* lizardfishes. Specifically, each of 2 *Synodus* species, *S. intermedius* (Agassiz, 1829) (Sand Diver) and *S. foetens* comprise 2 distinct cytochrome *c* oxidase I (COI) lineages.

The purpose of this study was to reconcile genetic lineages with the nominal species of western Atlantic *Synodus*. Through comparative morphological study, our first goal was to determine if the “extra” genetic lineages correspond with morphologically distinct species and, if so, to assess whether they represent previously synonymized or undescribed species. Herein, we resurrect and redescribe *Synodus bondi* Fowler, 1939, from the synonymy of *S. foetens* and describe *S. macrostigmus* as a new species distinct from *S. intermedius*. We establish neotypes for *S. intermedius* and *S. foetens* and redescribe both species. We discuss preliminary evidence of population structure within *S. foetens*, *S. synodus* (Red Lizardfish), *Saurida brasiliensis*, and *Trachinocephalus myops* (Snakefish) and species-level genetic structure within *Synodus poeyi* (Offshore Lizardfish). Finally, we provide a revised key for the 7 species of *Synodus* found in the western Atlantic.

Materials and methods

Specimens for genetic analysis were collected in Tobago (Trinidad and Tobago), Turks and Caicos Islands, the Bahamas, Curaçao, Belize, North Carolina, South Carolina, and Florida. Type material and additional specimens from other localities were examined from ANSP, MCZ, UF, FSBC, KU, and USNM (institutional abbreviations are listed at <http://www.asih.org/node/204>, accessed February 2012). Specimens examined are listed in appropriate species sections or in the Appendix.

Specimens were collected with the use of quinaldine sulfate, rotenone, or a pole spear during snorkeling or scuba diving, as well as by bottom trawling and hook and line fishing. For most specimens, field protocol involved taking digital photographs of fresh specimens

to document living color patterns, and subsequently a small sample of tissue from the trunk musculature for genetic analysis. Voucher specimens were fixed in 10% formalin and ultimately preserved in 75% ethanol for archival storage.

Measurements were taken to the nearest 0.1 mm with Mitutoyo digital calipers (Mitutoyo Corp., Japan²). Measurements and counts follow Hubbs and Lagler (1964) and Randall (2009), except as noted below. Length of the anterior-nostril flap was measured from the posterior tip of the anterior nostril to the distal end of the flap when depressed. For the *S. intermedius* group only, the length of the scapular blotch was measured on an anterior–posterior axis at its greatest expanse. For the *S. foetens* group only, the width of the adipose lid was measured as the maximum distance between the bony orbit and distal edge of the lid.

Numbers of vertebrae and dorsal-, anal-, pectoral-, and caudal-fin rays were counted from digital radiographs or preserved specimens. Scales flanking the dorsal- and anal-fin bases are half the size of other trunk scales and are reported as half-scales.

Tissue samples were stored in saturated salt buffer (Seutin et al., 1990). DNA was extracted from up to approximately 20 mg minced, preserved tissue through an automated phenol:chloroform extraction on an Autogenprep965 DNA extraction system (Autogen, Holliston, MA) using the mouse tail tissue protocol to a final elution volume of 50 μ L. In the polymerase chain reaction (PCR), 1 μ L of extracted DNA was used in a 10 μ L reaction with 0.5 U BioLine (Bioline USA, Inc., Boston, MA) Taq polymerase, 0.4 μ L 50 mM $MgCl_2$, 1 μ L 10 $\times$ buffer, 0.5 μ L 10 mM deoxyribonucleotide triphosphate, and 0.3 μ L 10 μ M each primer FISH-BCL (5'-TCAACYAATCAYAAAGATATYGGCAG) and FISH-BCH (5'-TAAACTTCAGGGTGACCAAAAAATCA). The PCR thermocycle protocol was: 1 cycle of 5 min at 95°C; 35 cycles of 30 s at 95°C, 30 s at 52°C, and 45 s at 72°C; 1 cycle of 5 min at 72°C; and a hold at 10°C. PCR products were purified with ExoSAP-IT (Affymetrix, Santa Clara, CA) with 2 μ L 0.2 $\times$ enzyme and incubated for 30 min at 37°C. The reaction was then inactivated for 20 min at 80°C. Sequencing reactions were performed with 1 μ L of this purified PCR product in a 10 μ L reaction that contained 0.5 μ L primer, 1.75 μ L BigDye reaction buffer (Life Technologies Corp., Carlsbad, CA), and 0.5 μ L BigDye in the thermal cycler for 30 cycles of 30 s at 95°C, 30 s at 50°C, 4 min at 60°C, and then were held at 10°C after completion of cycles. These sequencing reactions were purified with MultiScreen-HV plates (MAHVN4550; EMD Millipore Corp., Billerica, MA) according to the manufacturer's instructions and stored dry until analyzed. Sequencing reactions were analyzed on an Applied Biosystems 3730XL automated DNA sequencer (Life Technologies Corp.), and sequence trace

² Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

files were exported into Sequencher, vers. 4.7 (Gene Codes Corp., Ann Arbor, MI). With the Sequencher program, ends were trimmed from the raw sequences until the first and last 10 bases contained fewer than 5 base calls with a confidence score (phred score) lower than 30. After trimming, forward and reverse sequences for each specimen were assembled. Each assembled pair was examined and edited by hand, and each sequence was checked for stop codons. Finally, the consensus sequence (655 bp) from each contig was aligned and exported in a NEXUS file format with PAUP* software, vers. 4.0 beta 10 (sensu Swofford, 2003).

MEGA software, vers. 5.05, (Tamura et al., 2011) was used to generate a distance matrix of Kimura 2-parameter distances (Kimura, 1980) of genetic sequence similarity, from which a neighbor-joining tree (Saitou and Nei, 1987) was constructed. The neighbor-joining tree is not intended to reflect phylogenetic relationships. The label for each entry on the tree is our DNA number, and we include that number in the material examined sections and figure captions. Abbreviations used in DNA numbers reflect geographical location, expedition name, or institutions that provided COI sequences or specimens for genetic analysis: BAH=Bahamas; BLZ=Belize; CUR=Curaçao; FCC=Florida Cape Canaveral (specimens were from east coast of Florida); FWRI=Florida Fish and Wildlife Research Institute (specimens were from deep waters of the Gulf of Mexico); FDA=Food and Drug Administration (specimens are from Alabama, collected by the FDA); specimens held at National Museum of Natural History, Smithsonian Institution [USNM]; KU=Kansas University Fish Collection (specimens are from Belize); MOC=Miguel Oliver Caribbean (specimens are from deep water off Central America); SC=South Carolina; SMS=Smithsonian Marine Station at Ft. Pierce, Florida (specimens are from east coast of Florida); TCI=Turks and Caicos; TOB=Tobago. COI sequences are deposited in GenBank (accession numbers in text). GenBank numbers for COI DNA sequences of type material, when sequences are available, are provided in the appropriate species sections. Photos were taken with a Fujifilm (Fujifilm Corp., Tokyo) or Nikon (Nikon Corp, Tokyo) digital camera or a Zeiss digital camera in a Zeiss Discovery V20 dissecting microscope (Carl Zeiss AG, Oberkochen, Germany). Photo credits are given only for images taken by individuals other than the authors.

Results

To generate genetic distances, 79 COI sequences of Synodontidae from numerous western Atlantic localities were used. From these genetic distances, a neighbor-joining tree was constructed. Intra- and interspecific divergences are tabulated in Table 1. To show the neighbor-joining tree on a single page, 23 sequences were then eliminated (Fig. 1). Removal of the sequences had no effect on tree topology. Our data set

includes all 10 previously recognized species of western Atlantic Synodontidae—5 species of *Synodus*, 4 species of *Saurida*, and *Trachinocephalus myops*. Specimens originally identified as *Synodus intermedius* and *S. foetens* constitute 4 genetic lineages, 2 of which represent *S. intermedius* (Agassiz, 1829) and *S. foetens* (Linnaeus, 1766). One of the remaining lineages represents *Synodus bondi* Fowler, 1939, a species that Anderson et al. (1966) relegated to the synonymy of *S. foetens*. The fourth lineage represents a new species. Herein, we describe the new species, redescribe *S. intermedius*, *S. foetens*, and *S. bondi*, and designate neotypes for *S. intermedius* and *S. foetens*. Percentages in parentheses throughout their descriptions represent mean values for all specimens examined.

Synodus macrostigmus Fable, Luther, and Baldwin, new species

Proposed English common name: Largespot Lizardfish

Figures 1, 2A, 3 (A and B), and 4, Tables 1–3

Holotype

UF 182810 (formerly, FSBC 020548), 189 mm standard length (SL), off Panama City, Florida, 29°16'59.95'N, 85°53'12.94'W, 71–73 m, sta. 097, NMFS-Pascagoula Deepwater Pelagics Survey, 1 November 2007, Coll: M. M. Leiby.

Holotype COI sequence

GenBank sequence JX519377, UF 182810 (formerly FSBC 020548), DNA number FWRI 20548b.

Paratypes

UF 182811 (formerly, FSBC 020548), 1 specimen, 192 mm SL (paratopotype), same locality data as for holotype; UF 182812 (formerly FSBC 020596), 5 specimens, 145–185 mm SL, off St. Petersburg, Florida, 28°8'44.41'N, 84°38'56.29'W, 75–77 m, sta. 123, NMFS-Pascagoula Deepwater Pelagics Survey, 5 November 2007, Coll: M. M. Leiby; USNM 358546, 1 specimen, 205 mm SL, Yellowtail Reef, Alabama, 29°33'28.08'N, 87°27'42.12'W, 68 m, sta. USGS-AE-9701-080, USGS Pinnacle Project, 12 August 1997.

Paratype COI sequences

GenBank sequences JX519376 and JX519380, UF 182811 and UF 182812, respectively, DNA numbers FWRI 20548a and 20596, respectively.

Additional material (not DNA vouchers)

Alabama: UF 29771, 5; Florida (Gulf of Mexico): UF 29818, 1; UF 46974, 1; UF 121816, 1; UF 123421, 2; UF

Table 1

Average percent divergence in cytochrome c oxidase I (COI) among species of *Synodus* (Sy.), *Saurida* (Sa.), and *Trachinocephalus* (T.) in the western Atlantic. Divergences between *Synodus macrostigmus* and *S. intermedius*, between *S. foetens* and *S. bondi*, and between the 2 lineages of *S. poeyi* are highlighted in bold. N/A=not available.

	Sa. <i>brasilienis</i>	Sa. <i>caribbaea</i>	Sa. <i>normani</i>	Sa. <i>suspicio</i>	Sy. <i>bondi</i>	Sy. <i>foetens</i>	Sy. <i>intermedius</i>	Sy. <i>macrostigmus</i>	Sy. <i>poeyi</i> 1	Sy. <i>poeyi</i> 2	Sy. <i>saurus</i>	Sy. <i>synodus</i>	T. <i>myops</i>
<i>Sa. brasilienis</i> n=1	N/A												
<i>Sa. caribbaea</i> n=3	0.09	0.00											
<i>Sa. normani</i> n=4	0.21	0.20	0.01										
<i>Sa. suspicio</i> n=2	0.20	0.21	0.23	0.00									
<i>Sy. bondi</i> n=1	0.25	0.24	0.24	0.27	N/A								
<i>Sy. foetens</i> n=13	0.27	0.26	0.26	0.31	0.16	0.01							
<i>Sy. intermedius</i> n=15	0.27	0.26	0.25	0.26	0.21	0.23	0.00						
<i>Sy. macrostigmus</i> n=3	0.24	0.22	0.24	0.27	0.18	0.21	0.16	0.00					
<i>Sy. poeyi</i> 1 n=3	0.26	0.24	0.26	0.27	0.21	0.23	0.26	0.23	0.00				
<i>Sy. poeyi</i> 2 n=3	0.25	0.22	0.22	0.22	0.21	0.23	0.21	0.17	0.18	0.00			
<i>Sy. saurus</i> n=1	0.22	0.22	0.24	0.21	0.19	0.23	0.26	0.22	0.24	0.22	N/A		
<i>Sy. synodus</i> n=26	0.25	0.25	0.25	0.23	0.23	0.26	0.26	0.23	0.25	0.24	0.23	0.00	
<i>T. myops</i> n=4	0.28	0.27	0.26	0.26	0.24	0.23	0.27	0.27	0.25	0.27	0.23	0.26	0.01

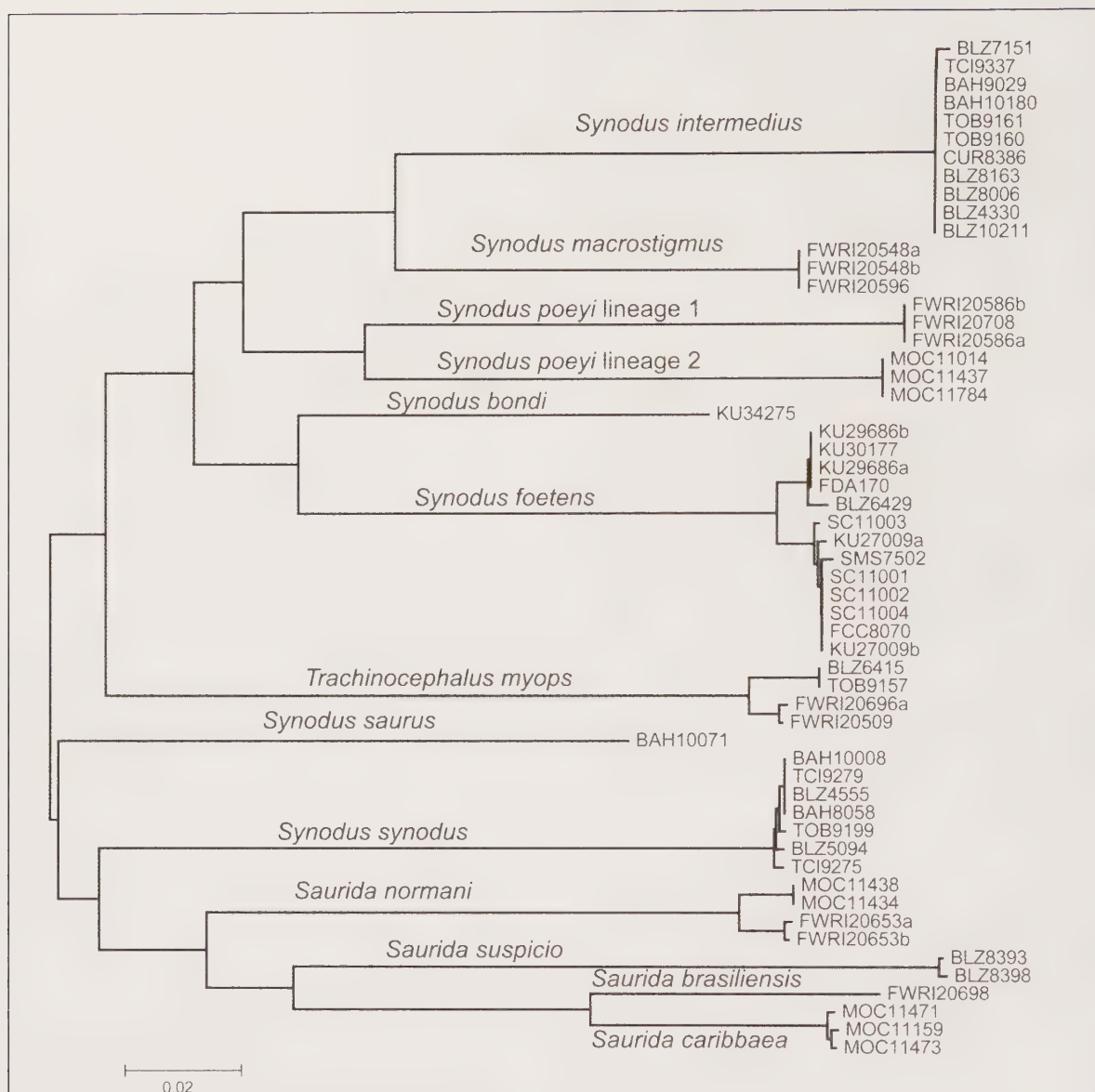


Figure 1

Neighbor-joining tree derived from 56 cytochrome *c* oxidase I sequences, showing genetically distinct lineages of Synodontidae in the western Atlantic. Abbreviations for DNA numbers are BAH=Bahamas; BLZ=Belize; CUR=Curaçao; FCC=Florida Cape Canaveral (specimens were from east coast of Florida); FWRI=Florida Fish and Wildlife Research Institute (specimens were from deep waters of the Gulf of Mexico); FDA=Food and Drug Administration (specimens are from Alabama, collected by the FDA-specimens held at National Museum of Natural History, Smithsonian Institution [USNM]); KU=Kansas University Fish Collection (specimens are from Belize); MOC=Miguel Oliver Caribbean (specimens are from deep water off Central America); SC= specimens collected off South Carolina; SMS=Smithsonian Marine Station at Ft. Pierce, Florida (specimens are from east coast of Florida); TCI=Turks and Caicos; TOB=Tobago.

146801, 1; UF 146657, 3; UF 152128, 7; UF 154795, 7; UF 169896, 1; UF 119194, 2; UF 123425, 2; UF 29799, 6; UF 147265, 1; UF 147286, 2; Florida (Atlantic): UF 111202, 5; Georgia: UF 123372, 1; UF 137046, 1; USNM 315754, 1; South Carolina: USNM 315532, 1; Mexico: UF 136960, 2; UF 136965, 1; USNM 18800, 3.

Diagnosis

A species of *Synodus* differentiated from its congeners by the following combination of characters: dorsal-fin rays 11 or 12 (rarely 11); anal-fin rays 11; total caudal rays 41–42; dorsal segmented caudal rays 9; ventral

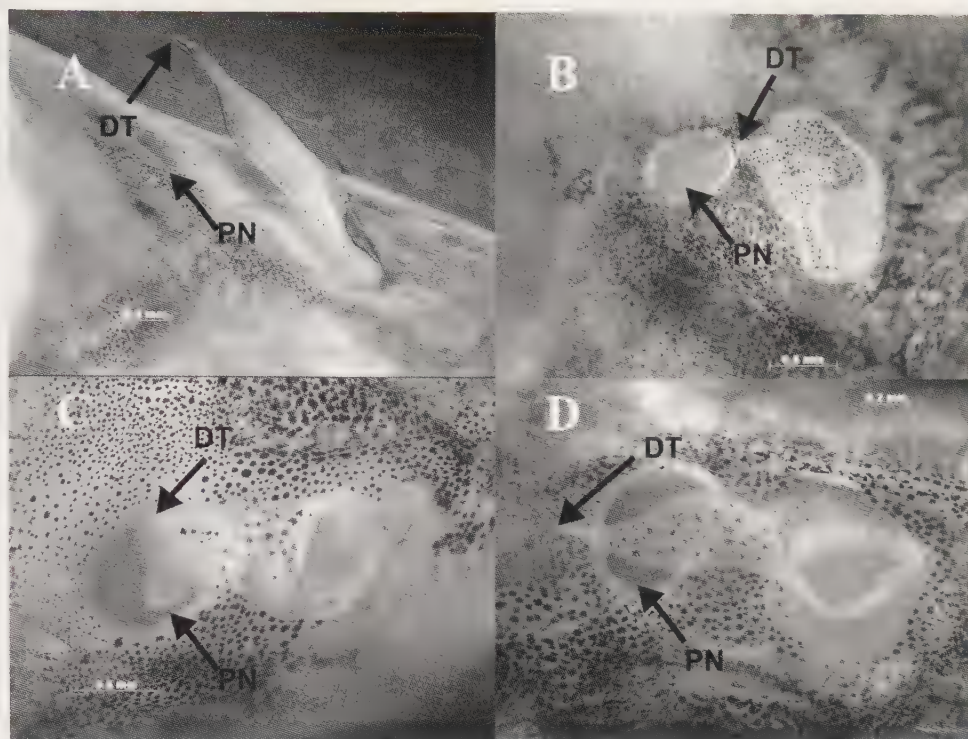


Figure 2

Anterior-nostril flaps in (A) *Synodus macrostigmus*, UF 182812, 185 mm SL; (B) *S. intermedius*, USNM 405469, 196 mm SL; (C) *S. foetens*, USNM 405414, 130 mm SL, photo by G. D. Johnson (USNM); and (D) *S. bondi*, USNM 389982, 123 mm SL, photo by G. D. Johnson. DT=distal tip of anterior nostril; PN=posterior nostril.

segmented caudal rays 10; dorsal procurrent caudal rays 12; ventral procurrent caudal rays 10–11; pelvic-fin rays 8; pectoral-fin rays 11 or 12; total vertebrae 47–49, modally 49; predorsal vertebrae 12 or 13; pored lateral-line scales 45–48; median predorsal scales 12 or 13; scale rows on cheek 4–6; eye large, 4.5–6.9% SL (16.7–24.7% head length [HL]); anterior nostril flap long, tapering distally and extending over posterior nostril when depressed, length of flap 2.7–4.9% HL; snout blunt in dorsal view; pelvic-fin length 21.6–25.2% SL. Caudal fin with dark pigment on anterior end of fork and posterior portion of ventral caudal lobe; dorsal caudal lobe pale with light pigment on posterior margin; shoulder with large, ovoid, black scapular blotch, length 14.2–19.0% HL; 6–9 dark bars on trunk; in life, adults gray to olive with unevenly distributed orange-yellow stripes along body.

Description

Description based on 52 specimens, 67.0–212.0 mm SL. Counts and measurements of holotype given in Table 2. Frequency distribution of pored lateral-line scales given in Table 3.

Dorsal-fin rays 11–12, rarely 11; anal-fin rays 11; total caudal-fin rays 41–42; dorsal segmented caudal rays 9; ventral segmented caudal rays 10; dorsal procurrent caudal rays 12; ventral procurrent caudal rays 10–11; pelvic-fin rays 8; pectoral-fin rays 11 or 12; total vertebrae 47–49, modally 49; predorsal vertebrae 12 or 13; scales ctenoid; pored lateral-line scales 45–48, modally 47; median predorsal scales 15 or 16; scales above lateral line to dorsal-fin base 3.5; scales below lateral line to anal-fin base 4.5.

Body elongate and cylindrical; depth at pelvic-fin origin 9.3–13.8% SL (12.1%); depth at anal-fin origin 8.3–10.7% SL (9.6%); caudal-peduncle depth 4.4–5.7% SL (5.1%); body width at dorsal-fin origin 11.2–15.3% SL (13.1%); HL 24.2–29.0% SL (26.3%); snout length 5.6–7.4% SL (6.4%) and 21.7–26.5% HL (24.3%); orbit diameter 4.5–6.9% SL (5.5%) and 16.7–24.7% HL (20.8%), orbit with bony ridge extending over anterodorsal margin; interorbital width 2.8–4.3% SL (3.6%) and 9.5–15.3% HL (13.8%).

Predorsal length 37.8–43.6% SL (40.4%); prepelvic length 32.2–36.5% SL (34.3%); preanal length 67.6–72.5% SL (70.4%); preadipose length 75.7–82.1% SL (79.3%); dorsal-fin base 15.0–18.2% SL (16.5%), longest



Figure 3

Comparison of coloration: (A) *Synodus macrostigmus*, holotype, UF 182810, coloration of live specimen; (B) *S. macrostigmus*, new species, holotype, UF 182810, 189 mm SL, coloration of preserved specimen (C) *S. intermedius*, neotype, USNM 398292, 285 mm SL, coloration of live specimen, photo by C. Boucher, NOAA; and (D) *S. intermedius*, neotype, USNM 398292, 285 mm SL, coloration of preserved specimen.



Figure 4

Distribution map *Synodus intermedius* and *S. macrostigmus*, new species. Symbols indicate sampling localities, not individual specimens. Dashed-line ovals highlight area of overlap in distribution of these species. Map by Robert Myers (Coral Graphics), reprinted with permission.

dorsal-fin ray 15.2–17.0% SL (16.1%); anal-fin base 13.0–15.5% SL (14.3%), longest anal-fin ray 6.9–9.4% SL (7.7%); pectoral-fin length 12.5–14.7% SL (13.5%); pelvic-fin length 21.6–25.2% SL (23.3%); caudal-peduncle length 9.9–16.7% SL (13.4%), caudal-fin length 16.5–21.5% SL (19.1%), ventral caudal lobe slightly longer than dorsal lobe.

Upper jaw slightly shorter than lower jaw, mouth oblique, forming an 8° angle with the horizontal body axis; upper-jaw length 13.7–17.6% SL (15.9%) and 55.8–63.8% HL (60.3%). Teeth thin, needlelike; upper jaw with 2 rows of teeth, teeth in inner row longer than teeth in outer row; lower jaw with 3 rows of teeth, size of teeth increasing medially, outer row covered by lips; posterior teeth in both jaws directed slightly anteriorly. Palatine with 3–4 rows of depressible teeth, teeth directed posteromedially. Tongue with 5 rows of posteriorly directed teeth, largest near anterior tip. Anterior nostril on level with median axis of orbit; posterior nostril same size and situated slightly dorsal to anterior nostril; anterior nostril with large, leaf-shaped flap that tapers distally, length of flap when depressed 0.8–1.2% SL (1.0%) and 2.7–4.9% HL (3.8%); anterior portion of posterior nostril occluded by basal rim of flap (Fig. 2A); posterior nostril without flap.

Cheek with 4–6 rows of large scales, modally 6; opercle with vertical row of 5–6 scales on anterior

margin and several scales posteriorly; predorsal scales extending anteriorly to a position approximately one orbit diameter posterior to eye; interorbital region naked. Dorsal and anal fins each flanked basally by 10–12 half scales, remainder of dorsal and anal fins without scales; large, diamond-shaped scales covering pelvic-fin base, remainder of pelvic fin and pectoral fin without scales; 6 rows of body scales extending onto base of caudal fin; upper and lower caudal lobes each with a single, enlarged, horizontally elongate scale.

Coloration

Before preservation (Fig. 3A) Head and dorsal half of trunk gray to greenish brown, ventral half of trunk pale; 6–8 dark brown markings along length of trunk laterally, at least some of them resembling wide crosses that are widest along lateral midline; markings on left and right portions of trunk connected to one another across dorsal midline to form saddles; trunk also with several thin orange-yellow stripes dorsally, stripes thicker or broken into orange blotches ventrally; groove above maxilla with stripe of black pigment from below anterior edge of orbit to posterior end of jaw; posterior edge of branchiostegal membrane pale yellow; scapular region with large black blotch of pigment partially hidden by operculum, length 3.8–4.9% SL (4.3%) and

Table 2

Counts and proportional measurements of the holotype and paratypes of *Synodus macrostigmus*, new species, and neotype of *S. intermedius*. Standard length present in millimeters; other measurement values in percentages of standard length; values in parentheses are percentages of head length.

	<i>Synodus macrostigmus</i> Holotype UF 182810	<i>Synodus macrostigmus</i> Paratype UF 182811	<i>Synodus macrostigmus</i> Paratype UF 182812	<i>Synodus macrostigmus</i> Paratype UF 182812	<i>Synodus macrostigmus</i> Paratype UF 182812	<i>Synodus macrostigmus</i> Paratype UF 182812	<i>Synodus macrostigmus</i> Paratype UF 182812	<i>Synodus macrostigmus</i> Paratype UF 182812	<i>Synodus macrostigmus</i> Paratype USNM 358546	<i>Synodus intermedius</i> Neotype USNM 398292
Standard length	189.0	192.0	185.0	149.0	162.0	172.0	156.0	205.0	285.0	
Vertebrae	49	49	48	49	47	49	49	47	49	
Dorsal-fin rays	12	12	12	12	12	12	12	12	12	
Anal-fin rays	11	11	11	11	11	11	11	11	11	
Pectoral-fin rays	12-12	12-12	12-11	12-12	12-12	11-12	12-12	11-11	13-13	
Pelvic-fin rays	8-8	8-8	8-8	8-8	8-8	8-8	8-8	8-8	8-8	
Caudal-fin rays	41	41	41	40	41	40	41	41	43	
Pored lateral-line scales	47	48	47	46	47	46	47	48	51	
Predorsal scales	15	15	15	Missing	Missing	15	14	16	17	
Cheek scales	6	6	6	6	6	Missing	6	6	7	
Body depth (pelvic origin)	11.0	11.9	9.7	12.7	11.6	10.7	9.3	12.3	15.1	
Body depth (anal origin)	9.8	10.3	8.8	9.7	9.5	8.6	8.3	9.4	10.2	
Caudal-peduncle depth	5.0	5.6	4.8	4.9	5.3	4.4	4.7	5.1	6.1	
Body width	14.0	13.0	13.0	13.5	14.0	12.2	12.5	13.5	15.6	
Head length	24.2	24.4	24.8	25.4	25.8	24.6	25.5	26.1	26.9	
Snout length	5.7 (23.7)	5.6 (23.0)	5.9 (23.8)	6.1 (23.9)	5.6 (21.7)	5.8 (23.4)	6.4 (24.9)	6.5 (24.9)	6.0 (22.8)	
Nostril-flap length	0.9 (3.9)	1.2 (4.9)	1.0 (4.1)	1.0 (4.1)	1.1 (4.1)	1.2 (4.9)	0.9 (3.7)	1.1 (4.4)	0.4 (2.2)	
Orbit diameter	5.0 (20.5)	5.1 (20.7)	5.3 (21.6)	6.0 (23.5)	5.9 (22.8)	5.8 (23.4)	5.5 (21.5)	5.3 (20.4)	3.6 (16.4)	
Interorbital width	3.7 (15.3)	3.7 (15.3)	3.7 (14.8)	3.8 (13.9)	3.5 (13.5)	3.5 (14.2)	3.3 (12.8)	3.8 (14.7)	4.6 (17.5)	
Upper-jaw length	15.2 (62.3)	14.8 (60.4)	15.2 (61.2)	15.5 (61.0)	14.6 (56.7)	13.7 (55.8)	15.9 (62.1)	15.5 (59.3)	16.2 (59.4)	
Scapular-blotch length	4.1 (17.0)	4.6 (18.8)	3.9 (14.8)	3.8 (14.8)	4.2 (16.1)	4.2 (16.9)	4.0 (15.6)	4.3 (16.5)	2.4 (10.4)	
Predorsal length	38.7	37.8	40.1	39.9	39.6	39.5	39.2	40.0	40.8	
Preanal length	68.8	70.3	70.3	67.6	69.8	69.2	69.9	71.7	71.1	
Preadipose length	76.7	78.1	75.7	77.2	80.2	80.2	78.8	79.5	83.2	
Prepelvic length	34.4	35.3	32.2	33.0	35.7	33.3	33.8	35.2	34.4	
Dorsal-fin base	16.5	15.2	15.0	16.7	15.6	15.0	15.3	17.5	17.2	
Longest dorsal ray	16.0	16.8	15.5	16.2	15.2	16.2	15.6	15.7	17.2	
Anal-fin base	14.7	14.8	13.8	15.3	14.0	13.3	13.0	14.4	15.5	
Longest anal ray	7.8	7.5	7.4	7.7	broken	7.1	9.4	7.7	9.6	
Pectoral-fin length	13.1	13.0	13.4	12.5	13.2	12.9	12.8	14.2	13.1	
Pelvic-fin length	22.6	24.7	21.8	23.0	21.6	23.5	24.9	23.3	26.2	
Caudal-peduncle length	14.1	16.7	15.6	15.2	15.3	9.9	10.4	11.3	15.7	
Caudal-fin length	19.0	18.4	19.0	20.0	21.5	20.1	16.5	18.7	17.5	

Table 3
Frequency distributions of counts of pored lateral-line scales in *Synodus macrostigmus*, new species ($n=51$), and *S. intermedius* ($n=52$).

	Pored lateral-line scales							
	45	46	47	48	49	50	51	52
<i>Synodus macrostigmus</i>	4	12	27	8	–	–	–	–
<i>Synodus intermedius</i>	–	–	–	–	7	16	23	6

14.2–19.0% HL (16.4%); dorsal fin not erect in available photographs (Fig. 3A), but depressed fin pale yellow with oblique rows of dark pigment; adipose fin pale with at least one dark marking dorsally; pectoral fin pale with approximately 6 wavy, irregular bars of dark brown pigment; pelvic fins bright yellow; anal fin yellow; center of caudal fin (at anterior end of fork) and posterior portion of ventral caudal lobe dark gray to brown; dorsal caudal lobe pale with light, dusky pigment on posterior margin; dorsal caudal lobe with 2–3 small brown bars on procurent rays.

In preservative (Fig. 3B) Trunk tan to light brown dorsally, pale ventrally; dark markings along trunk present but faded in some specimens; black pigmentation on scapular region, head, and caudal fin (described in the previous paragraph) easily visible; barring on pectoral fin indistinct.

Etymology

Synodus macrostigmus is named for its large, black scapular blotch. The species name is a Latinized conjunction of the Greek *macro*, meaning large or long, and *stigma*, meaning brand or mark.

Distribution

The holotype and paratypes are from the northeastern Gulf of Mexico off the coast of Florida from depths of 71–75 m. Additional specimens of this species, previously identified as *S. intermedius* in museum collections, are from the northern Gulf of Mexico off Alabama and Florida, Yucatan Mexico, and Atlantic coast off Georgia and South Carolina. All specimens were collected at depths below 28 m. The specimens from the deepest known collection, UF46974, are from the Gulf Coast of Florida at 194 m.

***Synodus intermedius* (Agassiz, 1829)**
English common name: Sand Diver
Figures 1, 2B, 3 (C and D), and 4, Tables 1–3

Saurus intermedius Agassiz in Spix and Agassiz, 1829:81, pl. 44. Type locality: “Brazil;” described

from specimen, 216 mm in total length in the Museo Monacensi, current whereabouts unknown; neotype herein designated, USNM 398292.

Saurus anolis Valenciennes in Cuvier and Valenciennes, 1850:483. Type localities: Martinique, Guadeloupe, and Bahia, Brazil; 2 types—MNHN A.8611, 390 mm, and MNHN B.1022, 400 mm.

Synodus cubanus Poey, 1876:143. Type locality: Cuba; one type—375 mm, current whereabouts unknown.

Holotype

No types known.

Designation of neotype

Agassiz (in Spix and Agassiz, 1829) described *Saurus intermedius* from a single specimen collected off Brazil (Kottelat, 1988). The original description is brief and provides little information to separate this species from a general *Synodus* body plan with the exception of the mention of transverse barring on the trunk, 55 mucous canal scales in the lateral line, a projected snout, and 12 pectoral- and anal-fin rays. The number of pored lateral-line scales is higher than the numbers observed in our study (49–52 scales); however, specimens of *S. intermedius* are known to have up to 55 lateral-line scales (Anderson et al., 1966; Anderson and Gehringer, 1975). The number of anal-fin rays (12) is also greater than the number we observed (11). This difference might be explained by a deep bifurcation in the last anal-fin ray that makes it appear to be 2 separate rays. The deep split is noted to result in miscounting (Anderson et al., 1966). There is no mention of caudal pigmentation or a scapular blotch.

Subsequent descriptions of *S. intermedius* by Günther (1864), Poey (1868), and Meek (1884) all included diagnostic features, such as a scapular blotch and caudal barring. Günther (1864) expressed frustration over the lack of diagnostic information in the original description. Kottelat (1988) was unable to locate the original type of *Saurus intermedius*. It may have been stored at the Zoologische Staatssammlung Munchen (ZSM), but the entire Spix and Agassiz collection housed there was destroyed in World War II (Kottelat,

1988). Or, it may be housed in the Museum d'Histoire Naturelle de Neuchâtel (MHNN), in Switzerland, where it has not been located. A color illustration of the holotype was published in Spix and Agassiz (1829, plate 44). The body shape, pigmentation, and barring on the caudal fin depicted in this illustration match those characters in later descriptions of *Saurus intermedius* and *Synodus intermedius* and in specimens recognized herein as *S. intermedius*. In light of our discovery of the similar *S. macrostigmus*, designation of a neotype is appropriate to clarify the taxonomic status of *S. intermedius*. We designate USNM 398292 from Brazil as a topologically equivalent neotype. We examined specimens of *Synodus intermedius* from Brazil and numerous localities in the Caribbean, and we found no significant morphological differences.

Note on authorship

Although *Synodus intermedius* was formally described in Spix and Agassiz (1829), Kottelat (1988) determined that Agassiz was the sole author of this name and the description was subsequently incorporated into this text. According to priority, the authorship of *S. intermedius* has been changed from (Spix and Agassiz, 1829) to (Agassiz, 1829) following the adopted format for other species described by Agassiz in the same work, including *Saurus longirostris* (Reis et al., 2003).

Neotype

USNM 398292, 285.0 mm SL, off northeastern Brazil, 0°13 48.00 N, 44°49 47.99 W, 62–64 m, sta. 67, Oregon II, 16 May 1975, field number BBC 1631, Coll: B. B. Collette.

Additional material

(DNA numbers and GenBank accession numbers for specimens that are vouchers are given in parentheses following catalog numbers). Florida: UF 146453, 3; UF 174147, 2; UF 234684, 1; UF 111225, 2; UF 116648, 5; UF 176286, 1; UF 152825, 1; UF 154795, 3; UF 152128, 3; UF 176286, 1; UF 29818, 4; USNM 38711, 1; USNM 35045, 1; Puerto Rico: UF 234199, 2; Bahamas Islands: USNM 405474, 1; USNM 405461 (BAH 9029: JX519387), 1; USNM 405462 (BAH 10043: JX519402), 1; USNM 405463 (BAH 10180: JX519386), 1; USNM 405464 (BAH 10181: JX519366), 1; Belize: USNM 327555, 1; USNM 404211 (BLZ 10211: JX519367), 1; USNM 405465 (BLZ 7151: JQ841412), 1; USNM 405468 (BLZ 8163: JQ841835), 1; USNM 405469 (BLZ 8006: JQ841836), 1; Bermuda: USNM 368585, 1; USNM 385983, 1; Brazil: USNM 398292, 1; Colombia: UF 123373, 1; UF 137038, 3; USNM 384339, 1; Curacao: USNM 405470 (CUR 8386: JQ842339), 1; French Guiana: UF 211584, 1; Guyana: UF 137049, 3; Honduras: UF 136971, 1; UF 123383, 1; Jamaica: UF 123615, 1;

UF 231377, 5; Saba, Leeward Islands: UF 207329, 2; Tobago, Trinidad and Tobago: USNM 405471 (TOB 9160: JQ843084), 1; USNM 405472 (TOB 9090: JQ843082), 1; UF 123378, 1; Turks and Caicos: USNM 405473, 1; Venezuela: UF 224467, 4; UF 123377, 1.

Diagnosis

A species of *Synodus* differentiated from its congeners by the following combination of characters: dorsal-fin rays 11–12; anal-fin rays 11; total caudal rays 40–42; dorsal segmented caudal rays 9; ventral segmented caudal rays 9–10; dorsal procurrent caudal rays 11–12; ventral procurrent caudal rays 9–10; pelvic-fin rays 8; pectoral-fin rays 11–13; total vertebrae 49–52, modally 50; pored lateral-line scales 49–52, modally 51; median predorsal scales 16 or 17; scale rows on cheek 6–8; HL 15.2–28.4% SL (26.6%); orbit diameter 3.6–6.4% SL (4.7%) and 13.4–22.5% HL (17.2%); interorbital width 2.8–5.3% SL (4.3%) and 10.1–19.4% HL (15.9%); flap on anterior nostril small and broad, length 1.5–3.6% HL (2.4%); snout triangular in dorsal view; pelvic-fin length 23.1–26.7% SL (24.9%). In preservative, 3 to 6 dark bars on caudal fin spanning upper and lower lobes; a small, rectangular-shaped, black scapular blotch (length 5.1–12.2% HL, mean 8.4%); 9 to 13 dark bars on trunk; in life, adults tan to olive and with unevenly distributed yellow stripes along body.

Description

Description based on 51 specimens, 59.2–285.0 mm SL. Counts and measurements of neotype given in Table 2. Frequency distribution of pored lateral-line scales given in Table 3.

Dorsal-fin rays 11–12; anal-fin rays 11; total caudal-fin rays 40–42; dorsal segmented caudal rays 9; ventral segmented caudal rays 9–10; dorsal procurrent caudal rays 11–12; ventral procurrent caudal rays 9–10; pelvic-fin rays 8; pectoral-fin rays 11–13; total vertebrae 49–52, modally 50; predorsal vertebrae 12 or 13; scales ctenoid; pored lateral-line scales, 49–52, modally 51, although counts of up to 55 have been reported (Anderson et al., 1966; Anderson and Gehringer, 1975); median predorsal scales 15–17; scales above lateral line to dorsal-fin base 3.5; scales below lateral line to anal-fin base 4.5.

Body cylindrical; depth at pelvic-fin origin 12.4–16.3% SL (14.1%); depth at anal-fin origin 8.7–11.7% SL (10.2%); caudal-peduncle depth 5.1–6.2% SL (5.7%); body width at dorsal-fin origin 9.7–16.2% SL (14.2%); HL 24.5–28.4% SL (26.6%); snout length 6.0–7.3% SL (6.7%) and 22.0–27.5% HL (24.7%), snout triangular in dorsal view; orbit diameter 3.6–6.4% SL (4.7%) and 13.4–22.5% HL (17.2%), orbit with bony ridge extending over anterodorsal margin; interorbital width 2.8–5.3% SL (4.3%) and 10.1–19.4% HL (15.9%).

Predorsal length 38.0–43.5% SL (41.0%); prepelvic length 33.4–37.9% SL (35.0%); preanal length 69.2–

76.4% SL (72.2%); preadipose length 75.5–84.5% SL (80.2%); dorsal-fin base 13.9–19.4% SL (16.8%), longest dorsal-fin ray, usually third, 14.5–20.0% SL (17.0%); anal-fin base 12.7–15.9% SL (14.2%), longest anal-fin ray, usually second, 7.7–10.7% SL (9.1%); pectoral-fin length 12.1–14.0% SL (13.1%); pelvic-fin length 23.1–26.7% SL (24.9%); caudal-peduncle length 8.5–19.4% SL (14.9%), caudal-fin length (only measured in 19 specimens because many specimens had damaged caudal fins) 16.1–22.5% SL (19.4%), ventral caudal lobe slightly longer than dorsal lobe.

Mouth terminal, upper jaw slightly oblique, forming an 8° angle with the horizontal body axis; upper-jaw length 14.7–18.1% SL (16.4%) and 53.9–64.2% HL (60.4%). Teeth needlelike; upper jaw with 2 rows of teeth, teeth in inner row longer than teeth in outer row; lower jaw with 3 rows of teeth, size of teeth increasing medially, outer row covered by lips; posterior teeth in both jaws directed slightly anteriorly. Palatine with 3–4 rows of depressible teeth, teeth directed posteromedially. Tongue with 5 rows of posteriorly directed teeth, largest near anterior tip. Anterior nostril on level with median axis of orbit; posterior nostril same size and situated slightly dorsal to anterior nostril; anterior nostril with small, spade-shaped flap, length of flap when depressed 0.4–1.0% SL (0.6%) and 1.5–3.6% HL (2.4%); anterior nostril flap does not reach posterior nostril (Fig. 2B); posterior nostril without flap.

Cheek with 6–8 rows of large scales, modally 7; opercle with vertical row of 6–8 scales on anterior margin and several scales posteriorly; predorsal scales extending anteriorly to a position approximately one orbit diameter posterior to eye; interorbital region naked. Dorsal and anal fins each flanked basally by 10–12 half scales, remainder of dorsal and anal fins without scales; large, diamond-shaped scales covering pelvic-fin base, remainder of pelvic fin and pectoral fin without scales; 5–7 rows of body scales extending onto base of caudal fin; upper and lower caudal lobes each with a single, enlarged, horizontally elongate scale.

Coloration

Before preservation (Fig. 3C) Head and dorsal half of trunk gray-green to brown, ventral half of trunk pale; specimens more than 200 mm SL with 9–13 dark brown bars along length of trunk laterally, bars more faint in smaller specimens and resemble wide crosses that are widest along lateral midline; markings on left and right portions of trunk connected to one another across dorsal midline to form saddles; trunk with several thin, golden-yellow stripes dorsally, with stripes becoming disrupted near lateral midline and forming distinct stripes again ventrally; groove above maxilla with stripe of black pigment from below anterior edge of orbit to posterior end of jaw; posterior edge of branchiostegal membrane yellow; scapular region with small rectangular black blotch of pigment partially hidden by operculum, length 1.4–3.3% SL (2.3%) and 5.1–

12.2% HL (8.4%); dorsal fin yellow-brown with multiple oblique rows of dark pigment; adipose fin brown; pectoral fin translucent with 4–5 diagonal bars of dark brown pigment; pelvic fins golden-yellow with darker pigment between rays; anal fin yellow; caudal fin light brown with 3–5 rows of dark pigmentation spanning both lobes, posterior fringes of fin dark brown.

In preservative (Fig. 3D) Trunk tan to light brown dorsally, pale ventrally; dark markings along trunk present but faded in some specimens; black pigmentation on scapular region and jaw easily visible; barring on caudal fin less distinct in older specimens; barring on dorsal fin faded and pigmentation on pectoral and pelvic fins indistinct.

Distribution

Synodus intermedius was described originally from “the inlets and river outflows of Brazil” (Agassiz in Spix and Agassiz, 1829). The species also occurs widely throughout the western Atlantic. Specimens examined in this study are from Bermuda, the Gulf of Mexico, and the eastern coasts of the United States, Puerto Rico, Saba, Leeward Islands, Belize, Venezuela, Colombia, French Guiana, Guyana, Brazil, and Trinidad and Tobago (Fig. 4). Specimens are known from depths up to 183 m, but most specimens have been collected at depths <60 m.

Comparisons of *Synodus macrostigmus*, *S. intermedius*, and congeners

The anterior-nostril flap in *S. macrostigmus* is significantly larger (2.7–4.9% HL, mean 3.8%) than that flap of *S. intermedius* (1.5–3.6% HL, mean 2.4%) and tapers distally (ends more abruptly in *S. intermedius*—Fig. 2, A and B). *Synodus macrostigmus* on average possesses a larger orbit diameter (20.8% versus 17.2% HL) and more narrow interorbital (width 13.8% versus 15.9% HL). It possesses a more blunt snout than does *S. intermedius* (Fig. 3, A–D) and has fewer lateral-line scales (45–48, modally 47, versus 49–52, modally 51, in *S. intermedius*) (Table 3). Dark pigment on the caudal fin in *S. macrostigmus* is restricted primarily to the center of the fin and ventral lobe, whereas *S. intermedius* has a distinctive banded pattern with 3 to 6 bars. The scapular blotch in *S. macrostigmus* is much larger and more ovoid than the miniscule, rectangular marking in *S. intermedius*, mean length of blotch 16.4% HL in *S. macrostigmus* and 8.4% HL in *S. intermedius*.

Additional fresh specimens of the new species are needed to verify differences in color patterns, but, in available material, *S. macrostigmus* has orange lateral stripes and markings on the trunk and *S. intermedius* has yellow stripes (Fig. 3, A and C). Specimens of *S. intermedius* more than 200 mm SL also appear to have more vertical bars along the trunk (9–13) than do large specimens of *S. macrostigmus* (6–8). Finally, *S. macrostigmus* has not been collected at depths shall-

lower than 28 m, whereas nearly half of the specimens of *S. intermedius* examined are from those depths. *Synodus macrostigmus* generally inhabits deeper waters (mean depth 96.5 m) than does *S. intermedius* (mean depth 49.3 m), but they co-occur at many depths. For example, 4 specimens of *S. intermedius* and 1 specimen of *S. macrostigmus* (UF 29818) were collected in a single trawl off Florida.

From their congeners, *S. macrostigmus* and *S. intermedius* can be differentiated from *S. poeyi* by anterior dorsal-fin rays that do not extend beyond the distal tips of succeeding rays when the fin is depressed and from *S. saurus* (Bluestripe Lizardfish), *S. bondi*, *S. foetens*, and *S. synodus* in having fewer lateral-line scales (45–48 in *S. macrostigmus*, 55 or more in the other species).

Remarks

Two previously described species are currently recognized as synonyms of *Synodus intermedius* (Agassiz, 1829): *Saurus anolis* (Valenciennes in Cuvier and Valenciennes, 1850) and *Synodus cubanus* Poey, 1876. Valenciennes described *Saurus anolis* in 2 brief paragraphs in Cuvier and Valenciennes (1850), but he did not mention a scapular blotch and compared the specimens only with *S. synodus*. Type material was deposited in the Muséum National d'Histoire Naturelle (MNHN) in Paris; 2 syntypes exist in this material, one dried (MNHN A-8611) and one in alcohol (B-1022) (Bertin and Estève, 1950). The wet specimen appears to be *S. intermedius* on the basis of caudal barring and remnants of a miniscule scapular blotch. Diagnostic features are not discernible on the dried syntype.

Albert K. L. G. Günther purportedly synonymized *Saurus anolis* with *Synodus intermedius* before 1868 (Poey, 1868); however, no published reference has been located. Meek (1884) recognized *Saurus anolis* as valid in his systematic review of Synodontidae in the western Atlantic, but he stated the original description is "so insufficient that no certain identification can be made" (Meek, 1884: 134). Anderson et al. (1966) listed *Saurus anolis* as a synonym of *Synodus intermedius* without providing discussion. We concur with Meek's assessment of the original description but recognize *Saurus anolis* as a synonym of *Synodus intermedius* on the basis of features of one of the MNHN *Saurus anolis* syntypes.

The second synonym, *Synodus cubanus*, was described as having caudal barring, yellow body stripes, short pelvic fins, and a scapular spot (Poey, 1876). The description was based on a 375-mm-SL specimen from Cuba, but the whereabouts of this specimen are unknown. Jordan (1884) identified a specimen from Florida (USNM 35045) as Poey's *S. cubanus*, but he noted that it matches the description of *S. intermedius* by previous authors (e.g., Günther, 1864). Our examination of USNM 35045 revealed a small scapu-

lar marking typical of *S. intermedius* and diagnostic morphological features, such as 51 lateral-line scales. We agree that *S. cubanus* Poey, 1876, is a synonym of *S. intermedius*.

Synodus foetens (Linnaeus, 1766)

English common name: Inshore Lizardfish

Figures 1, 2C, 5 (A and B), and 6, Tables 1, 4, and 5

Salmo foetens Linnaeus, 1766: 513 (12th ed.). Description based on Catesby, 1743; specimens sent by Dr. Alexander Garden of Charleston, South Carolina; no types designated.

Osmerus albidus Lacepède, 1803: 229. Name given in list and based on descriptions by Catesby and Linnaeus. Type locality: South Carolina; no types designated.

Coregonus ruber Lacepède, 1803: 243. Name given in list and based on description by Plumier. Type locality: Martinique; no types designated.

Esox salmoneus Mitchill, 1815: 442. Type locality: New York Bay; described from specimens, 203–229 mm in total length; no types designated.

Saurus longirostris Agassiz in Spix and Agassiz, 1829: 80, pl. 43. Type locality: Brazil; described from specimens, 178–216 mm in total length; current whereabouts unknown.

Saurus mexicanus Cuvier, 1829: 314. Type locality: Gulf of Mexico; no types designated.

Saurus spixianus Poey, 1860: 304. Type locality: Cuba; one type—MCZ 6884, 330 mm.

Holotype

No types known.

Designation of neotype

Linnaeus (1766) described *Salmo foetens* from material collected off the coast of South Carolina. Type material is not present in known collections of Linnaean specimens (Wheeler, 1985; 1991), and, although the original description is vague, it indicates the presence of 12 anal-fin rays. We believe that the genetic lineage of "*Synodus foetens*" in our data set that comprises specimens with 12 anal-fin rays is *Synodus foetens* (Linnaeus, 1766); the type locality of *Salmo foetens* provides corroborative evidence, because several specimens in our *Synodus foetens* lineage are from South Carolina. To stabilize the taxonomic status of *Synodus foetens* and distinguish it from *S. bondi*, formerly considered a synonym of *S. foetens* but resurrected herein (see entry for *S. bondi* below), we establish a neotype for *S. foetens*. We have selected USNM 405413 as the neotype on the basis of its collection off the type locality, South Carolina.

Neotype

USNM 405413, 205 mm SL, South Carolina, 32°47'34.80"N, 79°39'46.80"W, 10 m, Sta. 20110526, 17 October 2011, Coll: P. Webster.

Neotype COI sequence

GenBank sequence JX519368, USNM 405413 (neotype), DNA number SC 11001

Additional material

(DNA numbers for specimens that are vouchers are given in parentheses following catalog numbers). Alabama: USNM 398343 (FDA 170: JX519375), 1; USNM 358612, 6; Georgia: UF 143583, 1; Florida: KU 29686 (KUIT 3949: JX519400, KUIT 3950: JX519401), 2; UF 177024, 1; UF 177327, 3; UF 177249, 1; USNM 160462, 3; USNM 57123, 1; USNM 38710, 1; USNM 405452, 15; USNM 405450 (SMS 7502: JQ842743), 1; USNM 405451 (FCC 8070: JQ841978), 1; Louisiana: UF 99242, 2; USNM 185713, 2; Mississippi: UF 137002, 3; Maryland: USNM 125789, 1; New Jersey: USNM 399108, 1; USNM 395747, 1; North Carolina: KU 27009 (KUIT 1127: JX519409, KUIT 1128: JX519410), 2; UF 5239, 3; UF 77354, 2; UF 178337, 9; South Carolina: UF 44476, 2; UF 39667, 1; UF 39650, 6; USNM 25998, 2; USNM 405414 (SC11002: JX519369, SC11003: JX519370), 2; USNM 405475 (SC11004: JX519371), 1; USNM 405449, 2; Texas: KU 30177 (KUIT 5069: JX519411), 1; UF 54575, 10; Bahamas Islands: UF 200425, 1; Belize: BLZ 6429: JQ841024 (tissue only), 1; Bermuda: USNM 337726, 3; Cuba: MCZ 6884, 1; USNM 331820, 1; Jamaica: UF 123664, 1; St. Martin, Leeward Islands: UF 205900, 1; Mexico: UF 125765, 1; UF 123640, 1; UF 7108, 1; UF 123660, 1; Puerto Rico: UF 137023, 1.

Diagnosis

A species of *Synodus* distinguished from all congeners by the following combination of characters: dorsal-fin rays 10–12, rarely 10; anal-fin rays 11–13, rarely 11; pectoral-fin rays 11–13; total caudal-fin rays 40–41; dorsal segmented caudal rays 9–10; ventral segmented caudal rays 9; dorsal procurent caudal rays 11–12; ventral procurent caudal rays 11; vertebrae 59–62; lateral-line scales 59–63, modally 60; predorsal scales 20–30; scale rows above the lateral line to dorsal-fin base 5.5–6.5; HL 23.5–28.0% SL; snout long and triangular (length 6.0–8.3% SL, mean 6.8%, and 24.5–31.9% HL, mean 27.1%), tip slightly rounded; anterior-nostril flap broad and triangular, length 1.7–3.9% HL (3.0%); orbit diameter 3.3–5.3% SL (3.9%) and 11.6–20.1% HL (15.6%); interorbital area wide (width 9.2–18.5% HL, mean 14.6%); adipose lid around orbit narrow (width 1.9–5.2% HL, mean 3.5%); dorsal-fin base 9.2–12.7% SL, mean 11.3%, equal in length to or shorter than anal-fin base (9.6–14.7% SL, mean 12.1%); posterior

tip of pectoral fin not extending to pelvic-fin origin; color in preservation: trunk dark tan to brown dorsally, paler ventrally; 6–8 dark, vertical cross-shaped markings along trunk in specimens <100 mm SL, crosses disappearing or becoming indistinct dark patches in larger specimens; dark pigment present along posterior margin of ventral portion of upper caudal-fin lobe and along entire posterior margin of lower lobe, sometimes extending onto main portion of ventral lobe; dorsal half of adipose fin dark; in life, adults olive to tan.

Description

Description based on 52 specimens, 58.7–380.0 mm SL. Counts and measurements of neotype given in Table 4. Frequency distribution of anal-fin rays given in Table 5.

Dorsal-fin rays 10–12, rarely 10; anal-fin rays 11–13, rarely 11; total caudal-fin rays 40–41; dorsal segmented caudal rays 9–10; ventral segmented caudal rays 9; dorsal procurent caudal rays 11–12; ventral procurent caudal rays 11; pectoral-fin rays 11–13, pelvic-fin rays 8; total vertebrae 59–62; predorsal vertebrae 17–19; scales ctenoid; pored lateral-line scales 59–63, modally 60; median predorsal scales 20–30; scale rows above the lateral line to dorsal-fin base 5.5–6.5; scales below lateral line to anal-fin base 6.5.

Body cylindrical and elongate; depth at pelvic-fin origin 7.5–14.2% SL (11.8%); depth at anal-fin origin 6.2–10.5% SL (8.4%); caudal-peduncle depth 4.5–5.7% SL (5.1%); body width at dorsal-fin origin 8.7–14.2% SL (11.3%); HL 23.5–28.0% SL (25.2%); snout length 6.0–8.3% SL (6.8%) and 24.5–31.9% HL (27.1%), snout long and pointed, tip rounded in dorsal view; orbit diameter 3.3–5.3% SL (3.9%) and 11.6–20.1% HL (15.6%), orbit with bony ridge extending over anterodorsal margin and with narrow adipose lid on its posterior edge, adipose lid width 0.5–1.3% SL (0.9%) and 1.9–5.2% HL (3.5%); interorbital region wide, width 2.3–5.2% SL (3.7%) and 9.2–18.5% HL (14.6%).

Predorsal length 41.2–48.7% SL (44.6%); prepelvic length 32.1–40.3% SL (37.1%); preanal length 71.9–80.1% SL (76.0%); preadipose length 77.3–86.1% SL (81.5%); dorsal-fin base 9.2–12.7% SL (11.3%), longest dorsal-fin ray, usually third, 13.0–16.5% SL (15.0%); anal-fin base 9.6–14.7% SL (12.1%), longest anal-fin ray, usually third, 6.7–9.9% SL (8.3%); pectoral-fin length 10.9–13.7% SL (12.0%); pelvic-fin length 17.7–22.6% SL (20.1%); caudal-peduncle length 8.8–14.0% SL (10.8%), caudal-fin length (only measured in 27 specimens because many specimens had damaged caudal fins) 14.1–19.5% SL (17.1%), caudal lobes generally same length.

Mouth terminal, upper jaw slightly oblique, forming a 10° angle with the horizontal body axis, upper jaw extending anterior to lower jaw; upper-jaw length 13.3–17.2% SL (15.5%) and 55.0–65.2% HL (61.1%). Teeth needlelike; upper jaw with 2 rows of teeth, teeth in inner row longer than teeth in outer row; lower jaw with 3 rows of teeth, size of teeth increasing medially,

Table 4

Counts and proportional measurements of the holotype and paratype of *Synodus bondi* and the neotype of *S. foetens*. Standard length presented in millimeters; other measurement values in percentages of standard length; values in parentheses are percentages of head length.

	<i>Synodus bondi</i> Holotype ANSP 68634	<i>Synodus bondi</i> Paratype ANSP 68635	<i>Synodus foetens</i> Neotype USNM 408413
Standard length	220.0	155.9	205.0
Vertebrae	60	—	62
Dorsal-fin rays	13	12	14
Anal-fin rays	10	10	12
Pectoral-fin rays	13–12	14–13	14–14
Pelvic-fin rays	8–8	8–8	8–8
Caudal-fin rays	42	42	42
Pored lateral-line scales	60	59	62
Predorsal scales	24	23	28
Cheek scales	6	6	7
Body depth (pelvic origin)	12.0	10.5	13.2
Body depth (anal origin)	10.8	8.8	8.5
Caudal-peduncle depth	6.0	5.9	5.4
Body width	13.2	12.1	11.8
Head length	25.7	24.7	25.3
Snout length	7.7 (30.0)	6.5 (26.3)	7.3 (28.9)
Nostril-flap length	0.8 (3.1)	0.7 (2.7)	0.6 (2.5)
Orbit diameter	3.2 (12.4)	3.4 (13.6)	3.7 (14.5)
Adipose-lid width	1.2 (4.7)	1.1 (4.6)	0.8 (3.1)
Interorbital width	4.3 (16.6)	3.8 (15.5)	3.7 (14.5)
Upper-jaw length	16.2 (62.9)	15.3 (62.0)	15.5 (61.4)
Predorsal length	44.4	44.1	43.6
Preanal length	77.3	76.4	74.7
Preadipose length	81.8	81.4	79.0
Prepelvic length	36.6	37.5	36.2
Dorsal-fin base	12.8	11.9	11.4
Longest dorsal ray	16.2	16.1	15.0
Anal-fin base	11.0	11.0	12.2
Longest anal ray	9.5	8.5	8.2
Pectoral-fin length	11.8	11.6	12.3
Pelvic-fin length	18.4	18.7	20.5
Caudal-peduncle length	10.7	13.9	9.4
Caudal-fin length	18.0	20.3	16.7

outer row covered by lips; posterior teeth in both jaws directed slightly anteriorly. Palatine with 3–4 rows of depressible teeth, teeth directed posteromedially. Tongue with 5 rows of posteriorly directed teeth, largest near anterior tip. Anterior nostril on level with median axis of orbit; posterior nostril same size and situated slightly dorsal to anterior nostril, nostrils almost on dorsal surface of snout; anterior nostril with small, triangular flap, length of flap when depressed 0.4–1.0% SL (0.8%) and 1.7–4.0% HL (3.0%); anterior nostril flap reaches center of posterior nostril when depressed (Fig. 2C); posterior nostril without flap.

Cheek with 7 rows of large scales, opercle with 3–5 vertical rows of 9–10 scales on anterior margin; predorsal scales extending anteriorly above anterior mar-

gin of preopercle; interorbital region naked. Dorsal and anal fins each flanked basally by 8–10 half scales, remainder of dorsal and anal fins without scales; 3 large, diamond-shaped scales covering pelvic-fin base, pelvic-fins flanked by a row of 4–6 half-scales laterally, remainder of pelvic fin and pectoral fin without scales; 7–9 rows of body scales extending onto base of caudal fin; upper and lower caudal lobes each with a single, enlarged, horizontally elongate scale.

Coloration

Before preservation (Fig. 5A) Head and dorsal half of trunk olive to brown, ventral half of trunk pale; 6–8 dark, vertical, cross-shaped markings along trunk in specimens <100 mm SL, with crosses disappearing or becoming indistinct dark patches in larger specimens; rows of light spots extending laterally over trunk; groove above maxilla with stripe of black pigment from anterior edge of orbit to posterior end of jaw; posterior edge of branchiostegal membrane pale yellow; dorsal fin brown with translucent membrane between rays; adipose fin tan with dark dorsal edge; pectoral fin translucent with dark pigment on dorsal edge; pelvic fin translucent to pale yellow; anal fin pale; dark pigment present along posterior margin of ventral portion of upper caudal-fin lobe and along entire posterior margin of lower lobe, sometimes extending onto main portion of ventral lobe.

In preservative (Fig. 5B.) Trunk dark tan to brown dorsally, paler ventrally; dark markings in small speci-

Table 5

Frequency distributions of counts of anal-fin rays in *Synodus bondi* (n=46) and *S. foetens* (n=52).

	Anal-fin rays			
	10	11	12	13
<i>Synodus bondi</i>	12	32	2	—
<i>Synodus foetens</i>	—	2	35	15

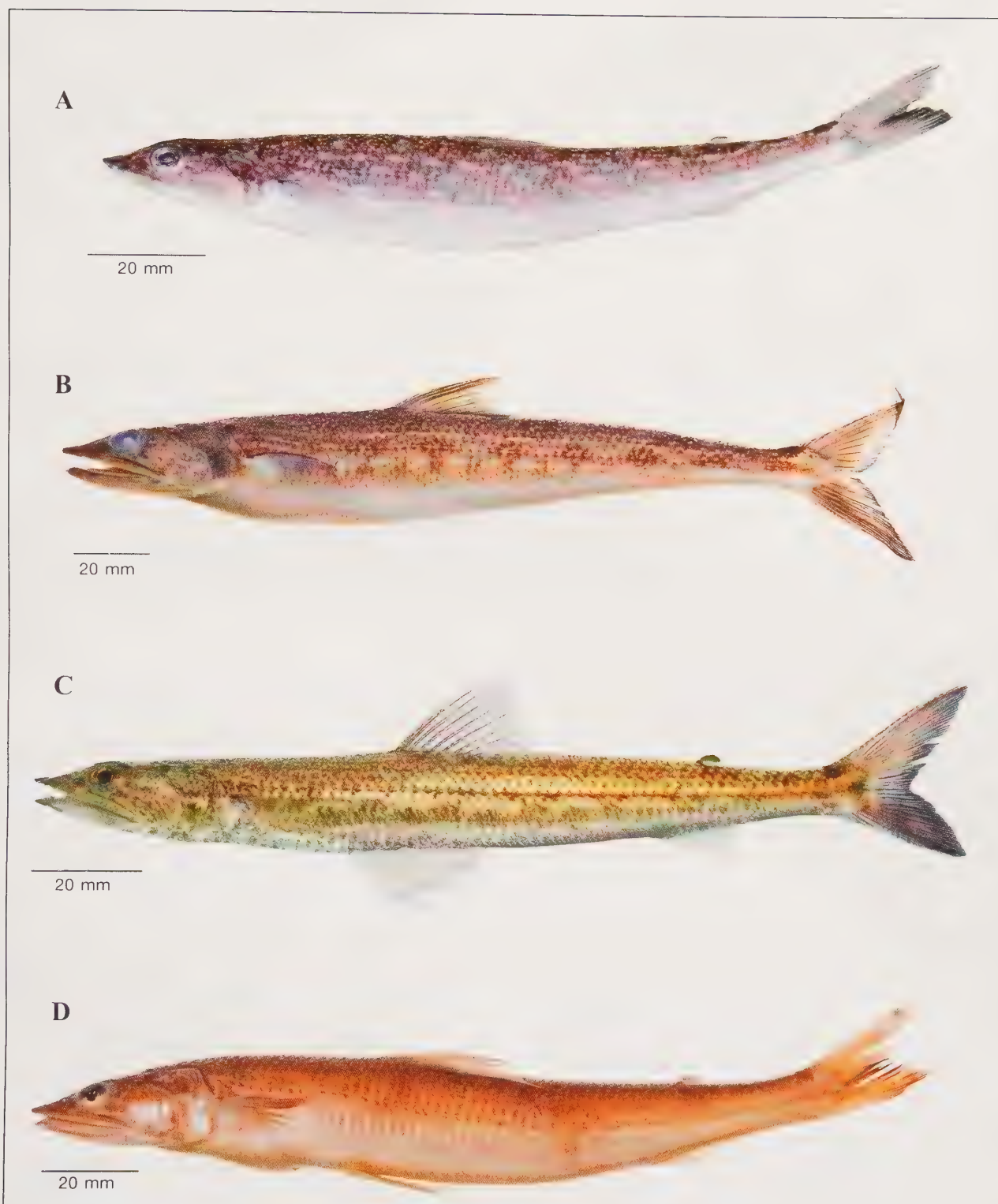


Figure 5

Comparison of coloration: (A) *Synodus foetens*, USNM 405414, 130 mm SL, coloration of live specimen; (B) *S. foetens*, neotype, USNM 405413, 205 mm SL, coloration of preserved specimen, photo by S. Raredon (USNM); (C) *S. bondi*, AMNH I-245350, 139 mm SL, coloration of live specimen, photo by D. R. Roberston (Smithsonian Institution) and J. Van Tassell (AMNH); and (D) *S. bondi*, holotype, ANSP 68634, 220 mm SL, coloration of preserved specimen.



Figure 6

Distribution map of *Synodus foetens* and *S. bondi*. Symbols indicate sampling localities, not individual specimens. Dashed-line oval highlights area of overlap in distribution of these species. Map by Robert Myers (Coral Graphics), reprinted with permission.

mens faded; black pigmentation on jaw, pectoral, and adipose fin easily visible; dark caudal-fin pigmentation less distinct in larger specimens (>280 mm SL).

Distribution

Synodus foetens was originally described from South Carolina (Linnaeus, 1766). Additional specimens examined span the mid- and south-Atlantic coast of the United States: New Jersey, Maryland, North Carolina, South Carolina, Georgia, and Florida; the Gulf of Mexico: Alabama, Mississippi, Louisiana, Texas, and Mexico; Bermuda; Bahamas; Cuba; Jamaica; Puerto Rico; and St. Martin in the Leeward Islands. One larval specimen was collected in Belize (Fig. 6).

Synodus bondi Fowler, 1939

Proposed English common name: Sharpnose Lizardfish

Figures 1, 2D, 5 (C and D), and 6, Tables 1, 4, and 5

Holotype

ANSP 68634, 220 mm SL, Kingston, Jamaica, field number JB35-K-1, Jan 1935, Coll: J. Bond.

Paratype

ANSP 68635, 156 mm SL, Kingston, Jamaica, field number JB35-K-1, Jan 1935, Coll: J. Bond.

Additional material

(DNA numbers for specimens that are vouchers are given in parentheses following catalog numbers). Belize: KU 34275 (KUIT 5804: JX519392), 1; UF 137041, 8; USNM 300454, 1; USNM 328256, 1; Brazil: UF 213980, 1; UF 123639, 6; French Guiana: UF 211687, 1; Guyana: UF 123665, 1; Haiti: USNM 133666, 1; Honduras: UF 123637, 1; Jamaica: UF 5191, 1; USNM 38538, 1; USNM 32076, 1; Panama: UF 75450, 1; UF 75707, 1; USNM 390121, 3; USNM 389847, 2; USNM 389982, 7; Tobago, Trinidad and Tobago: UF 123636, 3; Venezuela: UF 123656, 1; UF 123659, 1; USNM 405447, 1.

Diagnosis

A species of *Synodus* distinguished by the following combination of characters: dorsal-fin rays 11–12; anal-fin rays 10–12, rarely 12; pectoral-fin rays 12–14; total caudal-fin rays 42; configuration of caudal-fin rays always 12 dorsal procurent caudal rays + 10 segmented dorsal rays + 9 segmented ventral rays + 11 ventral

procurent rays; total vertebrae 56–60, modally 59; lateral-line scales 57–60, modally 60; predorsal scales 23–25; scales above the lateral-line to dorsal-fin base 5.5 or 6.5; HL 22.4–26.7% SL (25.2%); snout very long and triangular (length 6.3–9.1% SL, mean 7.3%, and 26.3–37.2% HL, mean 29.0%), tip sharply pointed; anterior nostril with long, narrow flap that tapers to a filament distally, length 2.6–5.3% HL (3.4%); orbit diameter 2.8–4.9% SL (3.5%) and 11.1–19.0% HL (13.8%); interorbital width 10.4–16.9% HL (15.5%); thick adipose lids on anterior and ventral margins of orbit (width 3.4–7.4% HL, mean 4.8%); dorsal-fin base 10.5–13.0% SL, mean 11.9%, usually longer than anal-fin base (9.6–12.7% SL, mean 11.0%). In preservative, body dark gray to reddish brown above the lateral axis, pale below; a few lateral stripes darker than background color sometimes present along length of body; no vertical bars on trunk; dark pigmentation present on margins of caudal fin, usually extending onto main portion of ventral lobe; dorsal half of adipose fin dark. Body pale green to tan in life.

Description

Description based on 45 specimens, 55.3–279.0 mm SL. Counts and measurements of type specimens given in Table 4. Frequency distribution of anal-fin rays given in Table 5.

Dorsal-fin rays 11–12; anal-fin rays 10–12, rarely 12; total caudal-fin rays 42; configuration of caudal-fin rays in all specimens examined: 12 dorsal procurent caudal rays + 10 segmented dorsal rays + 9 segmented ventral rays + 11 ventral procurent rays; pectoral-fin rays 12–14; pelvic-fin rays 8; total vertebrae 56–60, modally 59; predorsal vertebrae 15–18; scales ctenoid, lateral-line scales 57–60, modally 60; predorsal scales 23–25; scales above the lateral-line to dorsal-fin base 5.5 or 6.5; scales below lateral line to anal-fin base 6.5.

Body cylindrical and elongate; depth at pelvic-fin origin 8.8–15.9% SL (11.8%); depth at anal-fin origin 5.7–10.8% SL (8.9%); caudal-peduncle depth 3.5–6.5% SL (5.6%); body width at dorsal-fin origin 10.5–14.2% SL (12.7%); HL 22.4–26.7% SL (25.2%); snout length 6.3–9.1% SL (7.3%) and 26.3–37.2% HL (29.0%), snout long and triangular, tip pointed in dorsal view; orbit diameter 2.7–4.9% SL (3.5%) and 11.1–19.0% HL (13.8%), orbit with bony ridge extending over anterodorsal margin and with wide adipose lid on its posterior edge, adipose lid width 0.8–1.9% SL (1.2%) and 3.4–7.4% HL (4.8%); interorbital width 2.7–4.5% SL (3.9%) and 10.4–16.9% HL (15.5%).

Predorsal length 40.9–45.8% SL (43.9%); preopercle length 35.0–41.5% SL (38.6%); preanal length 75.0–81.3% SL (77.7%); preadipose length 80.0–86.4% SL (82.4%); dorsal-fin base 10.5–13.0% SL (11.9%), longest dorsal-fin ray, usually third, 14.0–17.2% SL (15.5%); anal-fin base 9.6–12.7% SL (11.0%), longest anal-fin ray, usually third, 7.0–9.6% SL (8.5%); pectoral-fin

length 11.0–13.2% SL (11.9%); pelvic-fin length 15.9–21.2% SL (18.8%); caudal-peduncle length 7.9–14.4% SL (12.1%), caudal-fin length (only measured in 31 specimens because many specimens had damaged caudal fins) 15.7–20.3% SL (17.6%), caudal lobes generally same length.

Mouth terminal, upper jaw slightly oblique, forming an 8° angle with the horizontal body axis, upper jaw extending anterior to lower jaw; upper-jaw length 14.6–17.0% SL (15.9%) and 58.0–70.1% HL (62.9%), lower jaw with fleshy nub at symphysis. Teeth needle-like; upper jaw with 2 rows of teeth, teeth in inner row longer than teeth in outer row; lower jaw with 3 rows of teeth, size of teeth increasing medially, outer row covered by lips; posterior teeth in both jaws directed slightly anteriorly. Palatine with 3–4 rows of depressible teeth, teeth directed posteromedially. Tongue with 4–5 rows of posteriorly directed teeth, largest near anterior tip. Anterior nostril slightly ventral to median axis of orbit; posterior nostril same size and situated slightly dorsal to anterior nostril; anterior nostril with long, narrow flap that tapers to a filament distally, length when depressed 0.7–1.4% SL (0.9%) and 2.6–5.3% HL (3.4%); anterior nostril flap extending beyond posterior nostril when depressed (Fig. 2D); posterior nostril without flap.

Cheek with 6 rows of large scales, opercle with 2 vertical rows of 7–9 scales on anterior margin and several scales posteriorly; predorsal scales extending anteriorly above anterior margin of preopercle; interorbital region naked. Dorsal fin flanked basally by 10–12 half-scales, anal fin flanked by 8–10 half-scales, remainder of dorsal and anal fins without scales; 3 large, diamond-shaped scales covering pelvic-fin bases, pelvic fins flanked laterally by 6 half-scales, remainder of pelvic fin and pectoral fin without scales; 7 rows of body scales extending onto base of caudal fin; upper and lower caudal lobes each with a single, enlarged, horizontally elongate scale.

Coloration

Before preservation (Fig. 5C) Head and dorsal half of trunk olive to golden-brown, ventral half of trunk pale; cross-shaped markings dispersed along trunk in specimens <100 mm SL, those markings not present in larger specimens; rows of light spots present on central region of trunk, spots darker in some specimens; groove above maxilla with stripe of black pigment from posterior edge of orbit to posterior end of jaw; dorsal-fin rays brown with translucent membrane between rays; adipose fin opaque, dorsal half dark; pectoral fin translucent with a few darker spots; pelvic fins translucent to pale yellow; anal fin pale; dark pigmentation present on margins of caudal fin, usually extending onto main portion of ventral lobe.

In preservative (Fig. 5D) Trunk dark orange-tan to brown dorsally, paler ventrally; dark markings in small specimens faded; lines on trunk faded or no longer visible; dark pigmentation on jaw and adipose fin visible; dark caudal-fin pigmentation less distinct in larger specimens (>280 mm SL).

Distribution

The holotype and paratype of *S. bondi* were collected off Kingston, Jamaica. Additional specimens of *S. bondi*, previously identified as *S. foetens*, are known from Jamaica, Haiti, Belize, Honduras, Panama, Trinidad and Tobago, Brazil, French Guiana, Guyana, and Venezuela. On the basis of the material examined, the distribution of this species is concentrated in the southern portions of the Caribbean (Fig. 6). No specimens currently are known from the United States, Mexico, Bahamas, or Bermuda.

Comparisons of *Synodus foetens*, *S. bondi*, and congeners

Synodus bondi was synonymized with *S. foetens* under the reasoning that "comparison of the type and paratype with specimens of *S. foetens* removes all doubt that *S. bondi* is identical to *S. foetens*" (Anderson et al., 1966: 73). The *S. foetens* discussed by Anderson et al. (1966) is undoubtedly the lineage we have identified as *S. foetens* because a majority of the specimens they examined possess 12–13 anal-fin rays and are from the United States and northern Caribbean. Anderson et al. (1966) noted that the apparent differences in counts between *S. foetens* and *S. bondi* for lateral-line scales and scale rows above the lateral line recorded by Fowler (1939) are incorrect. Their re-examination of the paratype of *S. bondi* revealed the presence of 60 (as opposed to Fowler's 54) lateral-line scales and 5 (instead of Fowler's 6) rows of scales above the lateral line. However, those counts were non-diagnostic in Fowler's species description, and additional reasoning for the synonymy was not provided.

Synodus bondi is, in fact, morphologically distinct from *S. foetens*. The snout of *S. bondi* ends in a sharper point than does the snout of *S. foetens* (Fig. 5) and is significantly longer (mean 29.0% HL in *S. bondi*, compared with 27.1% HL in *S. foetens*). The anterior-nostril flap in *S. bondi*, on average, is slightly longer than that flap in *S. foetens* (3.4% and 3.0% HL, respectively); however, the flap in *S. bondi* is narrow and tapers to a filament distally but in *S. foetens* is broad and triangular (Fig. 2, C and D). The upper jaw is longer in *S. bondi* than in *S. foetens*, 58.0–70.0% HL (63.0%) versus 55.0–65.2% HL (61.1%). The adipose lids surrounding the dorsal and ventral margins of the orbit are wider in *S. bondi* (mean 4.8% HL) than in *S. foetens* (mean 3.5% HL), making the orbit look superficially smaller in *S. bondi*. *Synodus bondi* usually possesses fewer anal-fin rays than does *S. foetens*

(10–12, usually 10 or 11, versus 12 or 13); as a result, the dorsal-fin base is usually longer than the anal-fin base in *S. bondi* (the opposite is true in *S. foetens*). In addition, the configuration of caudal-fin rays in *S. bondi* is consistently 12+10+9+11 in specimens examined, but it is more variable in *S. foetens* and other *Synodus* species. Finally, although the geographic ranges of these 2 species overlap in a swath across the central Caribbean, *S. bondi* otherwise has a more southern Caribbean distribution relative to *S. foetens*, which occurs northward to New York (Fig. 6).

Synodus bondi and *S. foetens* are distinguished from *S. synodus* by having a sharply pointed snout, pectoral fins that do not extend beyond the base of the pelvic fins, higher numbers of predorsal scales (20–30 versus 15–18), and no dark spot on the upper jaw. *Synodus bondi* and *S. foetens* differ from *S. saurus* by having 5 or 6 complete scale rows above the lateral line versus 3 and a snout that is longer than the diameter of the orbit. Finally, *S. bondi* and *S. foetens* are differentiated from *S. poeyi*, *S. intermedius*, and *S. macrostigmus* by having more than 55 lateral-line scales.

In the original description of *S. bondi*, Fowler (1939) noted that the type specimens have dark pigment on the isthmus and posterior margins of the branchiostegals. We did not observe this pigment in the ANSP types or additional material, but it may have faded in preservative. We have not examined fresh material beyond photographs.

Remarks

Although numerous synonyms exist for *Synodus foetens*, *S. bondi* is the only name that can be definitively associated with the additional genetic lineage of "*S. foetens*" in our material. Two nominal species, *Osmerus albidus* (Lacepède, 1803) and *Coregonus ruber* (Lacepède, 1803), were described only in brief paragraphs and lack known type material. The only diagnostic feature given in the original description for *C. ruber* is that it has a rounded snout. Based on the snout shape and lack of information of type material, neither name is applicable to specimens recognized herein as *S. bondi*. Mitchill (1815) described *Esox salmoneus* from New York without designating any type material. On the basis of the type locality, it is clear that this name also is not applicable to our *S. bondi* material. Cuvier (1829) described *Saurus mexicanus* from small, transparent specimens from the Gulf of Mexico without designating type material. These specimens were most likely larvae or small juveniles, but there is not enough detail in the original description to identify them to species. Agassiz (in Spix and Agassiz 1829) briefly described *Saurus longirostris* on the basis of 2 specimens from Brazil (deposited at ZSM) that have a short anal fin that comprises 12 rays and a very pointed snout. Kottelat (1988) was unable to find the type material of *Saurus longirostris* at ZSM or MHNN, and their whereabouts

Key to the western Atlantic species of *Synodus*

This key is modified from a provisional key for Synodontidae constructed by Russell (2003).

- | | | |
|----|---|-------------------------------------|
| 1a | Scales in lateral line 43 to 52..... | 2 |
| 1b | Scales in lateral line 54 to 65..... | 4 |
| 2a | Dorsal fin with anterior rays extending to, or usually beyond, tips of succeeding rays when depressed; lower jaw ending in fleshy knob; no black scapular blotch on shoulder under gill cover..... | <i>Synodus poeyi</i> |
| 2b | Dorsal fin with anterior rays not extending beyond, but occasionally extending to, tips of succeeding rays when depressed; lower jaw rounded anteriorly, without fleshy knob; black scapular blotch present on shoulder under gill cover | 3 |
| 3a | Caudal fin with 3–5 dark bars spanning both lobes; pored scales in lateral line 49–52; scapular blotch small and rectangular (length <12% HL); anterior-nostril flap broad and short, not tapering significantly posteriorly and not extending beyond posterior nostril when depressed..... | <i>Synodus intermedius</i> |
| 3b | Caudal fin without prominent dark bars but with dark pigment on lower lobe; pored scales in lateral line 45–48; scapular blotch large and ovoid (length >14% HL); anterior-nostril flap large, tapering posteriorly and extending beyond posterior nostril when depressed | <i>Synodus macrostigmus</i> new sp. |
| 4a | Three rows of complete scales between lateral line and base of dorsal fin | <i>Synodus saurus</i> |
| 4b | Four to 6 rows of complete scales between lateral line and base of dorsal fin..... | 5 |
| 5a | Snout rounded and blunt, its length less than diameter of eye; anal-fin base much shorter than dorsal-fin base; tip of pectoral fin extending well beyond base of pelvic fin; dark spot present on tip of upper jaw; predorsal scales 15 to 18..... | <i>Synodus synodus</i> |
| 5b | Snout triangular and pointed, its length greater than diameter of eye; anal-fin base slightly shorter to longer than dorsal-fin base; tip of pectoral fin falling short of or just reaching pelvic-fin base; no dark spot on tip of upper jaw; predorsal scales 20 to 30 | 6 |
| 6a | Anal-fin rays usually 10 or 11 (rarely 12); dorsal-fin base as long as or longer than anal-fin base; adipose lids around orbit thick; tip of snout sharply pointed; anterior-nostril flap narrow and tapering to filament distally; species currently known from off Central and South America, Jamaica and Haiti..... | <i>Synodus bondi</i> |
| 6b | Anal-fin rays usually 12 or 13 (rarely 11); dorsal-fin base usually shorter than anal-fin base (rarely same length); adipose lids around orbit narrow; tip of snout not sharply pointed, slightly rounded; anterior-nostril flap broad and triangular, not tapering to filament; species currently known from New York south to the Leeward Islands, the Gulf of Mexico, and Belize | <i>Synodus foetens</i> |

are unknown. Kottelat (1988) did find a specimen at MHNN collected off Brazil about the same time as Spix and Agassiz's (1829) *Saurus longirostris* (MHNN 793), which may be a syntype. However, as noted by Kottelat (1988), the length of that specimen does not match the lengths of *S. longirostris* recorded in the original description or in Agassiz's notes. Although this specimen could be the same one described by Fowler (1939) as *S. bondi* on the basis of its pointed snout, short anal fin, and collection locality (as noted previously, *S. bondi* is also known from Brazil), it would be imprudent to resurrect this name based on a specimen that may or may not be a primary type. Finally, we examined the holotype of another synonym, *Saurus spixianus* Poey, 1860 (MCZ 6884) and found that it has 13 anal-fin rays, a rounded snout, and morphometrics similar to those of *S. foetens*. Our observations, therefore, corroborate the synonymy of *Saurus spixianus* with *S. foetens*.

Discussion

Molecular variation

Our DNA barcoding analysis of Synodontidae in the Atlantic (Fig. 1) revealed 13 highly divergent lineages (average divergence in COI among lineages: 20.2%, range: 9.0–30.7%). Morphological examination of voucher specimens indicated that 10 of the lineages correspond to the following previously described species: *Saurida brasiliensis*, *S. caribbaea* (Smallscale Lizardfish), *S. normani* (Shortjaw Lizardfish), *S. suspicio* (Suspicious Lizardfish), *Synodus foetens*, *S. intermedius*, *S. poeyi*, *S. saurus*, *S. synodus*, and *Trachinocephalus myops*. Of the additional 3 lineages, 2 represent morphologically distinct species originally identified as *S. intermedius* and *S. foetens*. We describe *S. macrostigmus* for the former and resurrect *S. bondi* for the latter. The thirteenth lineage in the data set represents specimens from deep

water off Central America originally identified as *S. poeyi* (*Synodus poeyi* lineage 2 in Fig. 1). That lineage is 17.9% divergent from *S. poeyi* specimens from the Gulf of Mexico (*Synodus poeyi* lineage 1 in Fig. 1).

A comprehensive study of *S. poeyi* from throughout its range, similar to this study conducted for *S. intermedius* and *S. foetens*, should help clarify the taxonomy of that species and likely will result in the recognition of a new species or one resurrected from synonymy. Preliminary investigation of *Synodus synodus* and *Saurida brasiliensis* from Cape Verde (not included in Fig. 1) reveal approximately 5–6% divergences in COI from western Atlantic *Synodus synodus* and *Saurida brasiliensis*, indicating deep population structure or potential cryptic species in those lizardfish lineages. Initial investigation of some Pacific lizardfish species (genetic data not included in this article) indicates that *Trachinocephalus myops* from the Philippines is highly divergent in COI from western Atlantic *T. myops*—a finding that sheds doubt on the current circumtropical distribution of *T. myops* and the monotypy of *Trachinocephalus*. Further investigation of this genus worldwide is needed to evaluate species diversity.

The intrageneric genetic variation in COI in western Atlantic *Synodus* and *Saurida* is high compared to the variation observed for other marine fishes that have been analyzed. Ward et al. (2005) found the average intrageneric variation in 207 species of Australian fishes to be 9.93%, and Hubert et al. (2008) found an average 8.30% intrageneric distance for 193 species of Canadian freshwater fishes. Average intrageneric divergence in western Atlantic synodontids (20.5%) exceeds even the average intergeneric distance of 16.6% calculated by Kartavtsev (2011) for animal species in general. Interspecific and intergeneric distances are similar in western Atlantic synodontids (Table 1). Large divergences likely reflect older speciation events, but the factors that drive lizardfish evolution are unknown.

Geographic and population variation

Although a species phylogeny for synodontids is needed to hypothesize sister-group relationships and examine patterns of speciation in this family, we note that morphologically and genetically similar species, such as *S. foetens* and *S. bondi* or *S. intermedius* and *S. macrostigmus*, exhibit different geographical and, sometimes, depth distributions. *Synodus foetens* and *S. bondi* have nearly distinct geographical distributions (Fig. 6). *Synodus foetens* occurs off the East Coast of the United States, in the Gulf of Mexico, and in the central Caribbean; *S. bondi* occurs in coastal Central and South America northward to Haiti. The distribution for these species overlaps in Belize and eastward to Jamaica and Haiti (Fig. 6).

Having largely disjunct distributions that overlap in the central Caribbean is a pattern congruent with distributions observed in other predatory fish genera, such as *Scomberomorus* (mackerels) and *Rhizoprion-*

odon (sharpnose sharks). In *Scomberomorus*, *S. maculatus* occurs off the East Coast of the United States, in the Gulf of Mexico, and in the northern and northwestern Caribbean, whereas *S. brasiliensis* occurs in the southern and central Caribbean (Collette et al., 1978; Banford et al., 1999). These 2 species overlap off northern Central America and potentially in the southern Gulf of Mexico. Similarly, *Rhizoprionodon terraenovae* (Atlantic Sharpnose Shark) inhabits the Gulf of Mexico, northern Caribbean, and East Coast of the United States, whereas the closely related species, *R. porosus* (Caribbean Sharpnose Shark), occurs off South and Central America. These 2 species may overlap in the central Caribbean (Springer, 1964; Compagno et al., 2005). *Synodus foetens* and *S. bondi* do not appear to have different depth preferences because both species inhabit depths between the surface and 95 m.

The geographic distributions of *Synodus macrostigmus* and *S. intermedius* overlap (Fig. 4). *S. macrostigmus* is known from the eastern and southern Gulf of Mexico and East Coast of the United States, whereas *S. intermedius* inhabits the eastern Gulf of Mexico, East Coast of the United States, Bermuda, Bahamas, and the Caribbean. These overlapping distributions are similar to the distributions observed in 2 genetic lineages of the goby, *Bathygobius soporator* (Frillfin Goby), by Tornabene et al. (2010). Those authors did not describe the lineages as separate species because no morphological differences were found to corroborate the genetic data, but Tornabene and Pezold (2011) noted that the *B. soporator* lineages could represent recent divergence and ongoing speciation in the western Atlantic. However, because the genetic divergence was observed in mitochondrial DNA alone, they could not rule out the possibility of deep coalescence.

Unlike the gobies, *S. intermedius* and *S. macrostigmus* are morphologically distinct, and they exhibit different depth preferences. Although *S. macrostigmus* primarily inhabits depths below 28 m (mean 96.5 m), *S. intermedius* is found typically at shallower depths (mean 49.3 m). However, *S. intermedius* has a broad depth distribution and has been collected in deep water along with *S. macrostigmus* (i.e., UF29818). Further investigation is needed to ascertain possible reproductive barriers in the evolutionary history of these species and whether or not ecological speciation (e.g., Rocha et al., 2005) could have played a role.

The neighbor-joining tree (Fig. 1) also reveals evidence of population structure in some species. For example, *S. foetens* specimens from the Gulf of Mexico differ in COI by 1.2% from a specimen in Belize, and Caribbean specimens of *Trachinocephalus myops* differ genetically by 1.6% from 2 deepwater Gulf of Mexico specimens. Finally, within *Saurida normani*, specimens from the Gulf of Mexico differ from Central American specimens by 1.7%. Additional material and genetic analyses are needed to describe the population structure of western Atlantic lizardfishes.

Fisheries concerns

Globally, some synodontids are commercially important as food fishes. *Trachinocephalus myops*, *Synodus synodus*, *Saurida tumbil* (Greater Lizardfish), and *Harpadon nehereus* (Bombay Duck) are targeted throughout the Mediterranean, Indian Ocean, and Southeast Asia (Raje et al., 2004; Ghosh et al., 2009; Xu et al., 2011). In the western Atlantic, synodontid species are encountered almost exclusively as bycatch in recreational and commercial fisheries. As a result, they have received little attention from fisheries researchers and managers despite their role as significant fish predators in various ecosystems (Sweatman, 1984; Cruz-Escolano et al., 2005). As mentioned previously, *S. foetens* makes up 1.5–2.0% of shrimp-trawl biomass and is usually among the 10 most prevalent finfish encountered by shrimp trawlers in the Gulf of Mexico, Caribbean, and off the southeastern United States.¹ (Gutherz, 1987; Jeffers et al., 2008; Manjarrés et al., 2008). These studies also report collection of *S. intermedius* and *S. poeyi* in much smaller amounts.

Jeffers et al. (2008) found that *S. foetens* in the northern Gulf of Mexico has a very high instantaneous annual mortality related to bycatch in fisheries (F_b), ranging from 0.4–0.6/year, and estimated exploitation ratios (E) of 0.43–0.55. Exploitation ratios of more than 0.5 generally indicate heavy fishing pressure and potential for overexploitation (Gulland, 1977). These data indicate that, although *S. foetens* is not commercially targeted, it is still fully exploited as bycatch.

To date, only commercially targeted fish species have been evaluated quantitatively as bycatch in the northern Gulf of Mexico (Jeffers et al., 2008), and little is known about bycatch rates and their effects on populations for noncommercial species. Broad ecosystem-scale studies of the effects of bycatch are needed that include nontargeted but exploited species, such as lizardfishes. For such studies, as well as any management plans that might result from them, an accurate understanding of species diversity and distribution is essential. This study provides new insights into the systematics of lizardfishes in the western Atlantic that should be incorporated into future management plans and fisheries research programs.

Conclusions

The description of *Synodus macrostigmus* as a new species and the recognition of *S. bondi* as a valid species bring the total number of valid western Atlantic *Synodus* species to 7. The integration of molecular and morphological data greatly facilitated identification of the new species and recognition of *S. bondi* as valid. A thorough systematic revision of western Atlantic Synodontidae that incorporates both molecular and morphological data is needed, and it seems likely that additional new species may exist. Geographic variation

and population structure within this group also warrant further study.

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Appendix: Comparative material of western Atlantic Synodontidae examined in this study

In the lists below, the following sequence is observed: first, catalog number; second, DNA number; and third, GenBank accession number (the latter two numbers are shown within parentheses).

Synodus synodus USNM 405415 (BAH 8058: JQ839916), USNM 405416 (BAH 8059: JQ839915), USNM 405417 (BAH 9028: JX519403), USNM 405418 (BAH 9030: JX519388), USNM 405419 (BAH 10008: JX519382), USNM 405420 (BAH 10009: JX519383), USNM 405421 (BAH 10010: JX519384), USNM 405422

(BLZ 4026: JQ840361), USNM 405423 (BLZ 4027: JQ840360), USNM 405424 (BLZ 4555: JQ840362), USNM 405425 (BLZ 5094: JQ840726), USNM 405426 (BLZ 5133: JQ840727), USNM 405427 (BLZ 5159: JQ840729), USNM 405428 (BLZ 5240: JQ840728), USNM 405429 (BLZ 5214: JQ840730), USNM 405430 (BLZ 5455: JQ840725), USNM 405431 (BLZ 6297: JQ841025), USNM 405432 (TCI 9275: JX519404), USNM 405433 (TCI 9276: JX519405), USNM 405434 (TCI 9277: JX519389), USNM 405435 (TCI 9278: JX519390), USNM 405436 (TCI 9279: JX519406), USNM 405437 (TCI 9576: JX519408), USNM 405438 (TCI 9645: JX519407), USNM 405439 (TCI 9646: JX519391), USNM 405440 (TOB 9199: JQ843085).

Synodus poeyi FSBC 020586 (FWRI 20586a: JX519378, FWRI 20586b: JX519379), FSBC 020708 (FWRI 20708: JX519381), USNM 405441 (MOC 11014: JX519397), USNM 405442 (MOC 11437: JX519398), USNM 405443 (MOC 11784: JX519399).

Synodus saurus USNM 405444 (BAH 10071: JX519385).

Saurida brasiliensis FSBC 020698 (FWRI 20698).

Saurida caribbaea USNM 405445 (MOC 11159: JX519372), USNM 405446 (MOC 11471: JX519373).

Saurida normani FSBC 020653 (FWRI 20653a: JX519393), USNM 405453 (MOC 11434: JX519374), USNM 405454 (MOC 11438: JX519365).

Saurida suspicio USNM 405455 (BLZ 8329 JQ841833), USNM 405456 (BLZ 8393: JQ841834), USNM 405457 (BLZ 8397: JQ841786), USNM 405458 (BLZ 8398: JQ841832).

Trachinocephalus myops FSBC 020509 (FWRI 20509: JX519396); FSBC 020698 (FWRI 20698a: JX519394); USNM 405460 (BLZ 6415: JQ841030); USNM 405459 (TOB 9157: JQ843093); USNM 405459.

Abstract—The purpose of this study was to validate aging results of juvenile Shortfin Mako (*Isurus oxyrinchus*) by vertebral band counts. Vertebrae of 29 juvenile Shortfin Mako marked with oxytetracycline (OTC) were obtained from tag-recapture activities to determine centrum growth-band deposition. Tagging occurred off southern California from 1996 to 2010, and time at liberty of the 29 sharks ranged from 4 months to 4.4 years (mean=1.3 years). Growth information also was obtained from length-frequency modal analyses (MULTIFAN and MIXDIST) by using a 29-year data set of commercial and research catch data, in addition to a tag-recapture growth model (e.g., the GROTAG model). For vertebrae samples used for age validation, shark size at time of release ranged from 79 to 142 cm fork length (FL) and from 98 to 200 cm FL at recapture. Results from band counts of vertebrae distal to OTC marks indicate 2 band pairs (2 translucent and 2 opaque) are formed each year for Shortfin Mako of the size range examined. Length-frequency analyses identified 3 age-class modes. Growth rate estimates from 26.5 to 35.5 cm/year were calculated for the first age-class mode (85 cm FL) and from 22.4 to 28.6 cm/year for the second age-class mode (130 cm FL). Results from the tag-recapture growth model revealed fast growth during time at liberty for tagged fish of the 2 youngest age classes. Collectively, these methods suggest rapid growth of juvenile Shortfin Mako in the southern California study area and indicate biannual deposition of growth bands in vertebrae for the first 5 years.

Age validation of juvenile Shortfin Mako (*Isurus oxyrinchus*) tagged and marked with oxytetracycline off southern California

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For almost 3 decades, researchers in various parts of the world have focused on the problem of accurately interpreting age and growth in the Shortfin Mako (*Isurus oxyrinchus*) (e.g., Cailliet and Bedford, 1983; Cailliet et al., 1983; Pratt and Casey, 1983; Casey and Kohler, 1992; Campana et al., 2002; Bishop et al.¹; Ribot-Carballal et al., 2005; Bishop et al., 2006; Natanson et al., 2006; Ardiczone et al., 2006; Maia et al., 2007; Cerna and Licandeo, 2009; Okamura and Semba, 2009; Semba et al., 2009). Driving these efforts is the need to better assess the vulnerability of Shortfin Mako to harvest in commercial and recreational fisheries and as bycatch in longline and driftnet fisheries from high-seas fleets (Stevens, 2008). Studies of the demographic

dynamics of sharks have shown that average age at first maturity and the relative rate of growth that determines this parameter is one of the leading factors that affect the ability of most sharks to rebound from harvest pressures (Smith et al., 1998; Cortés, 2002; Garcia et al., 2008). Accurate age determinations also are necessary for calculations of growth and mortality rates, age at recruitment, and longevity.

The Shortfin Mako is an epipelagic species distributed in temperate and tropical seas worldwide (Compagno, 2001) and seldom found in water temperatures lower than 13–17°C (Casey and Kohler, 1992; Stevens, 2008). Shortfin Mako occur off the U.S. West Coast principally off California and Oregon, and catches are associated primarily with warm sea-surface temperatures from 15° to 25°C (PFMC, 2011). Most Shortfin Mako off the U.S. West Coast are sexually immature, and high recapture rates for tagged juveniles show that young individuals remain for about 2 years in nearshore California waters (Taylor and Bedford, 2001), where they are more frequently taken in the summer months and are only

¹ Bishop, S. D. H., M. P. Francis, and C. Duffy. 2004. Age, growth, maturity, longevity and natural mortality of the Shortfin Mako shark (*Isurus oxyrinchus*) in New Zealand waters. Working Paper SCTB17, BIO-4, National Institute of Water and Atmospheric Research, New Zealand, Ministry of Fisheries, NZ, 34 p. Presented at the 17th Meeting of the Standing Committee on Tuna and Billfish (SCTB), Majuro, Marshall Islands, 9–18 August 2004.

rarely found below the thermocline (Holts and Bedford, 1993). Large fish approaching 200 cm fork length (FL) disappear from the catch and presumably move offshore to a more oceanic and highly migratory existence, where most males are mature but females are not (Mollet et al., 2000; Joung and Hsu, 2005; Semba et al., 2011).

Researchers who study the age and growth of this species have used pairs of alternating bands of different mineralization in vertebral centra to estimate age. These estimates differ depending on assumptions about the number of band pairs that represent a single year of growth. Bishop et al. (2006) noted that despite different conclusions in these studies, all of them appear to have produced relatively similar growth curves if the same rate of band deposition was assumed. This finding indicates that techniques used by different research groups to identify countable band pairs are generally alike, with the greatest difference being assumptions about rates of band deposition. Smaller disparities may be due to ontogeny, geographic variability, divergent methods of preparing and interpreting vertebral banding patterns, difficulties in interpreting banding patterns, differences in sample sizes, or limitations of the growth models used (Bishop et al., 2006).

Although considerable advances have been made in determination of age and growth of Shortfin Mako, questions remain as to why current length-at-age models underestimate growth of young fish, especially fish ≤ 200 cm FL (Pratt and Casey, 1983; Bishop et al.¹; Maia et al., 2007). Bishop et al. (2006) suggested that this discrepancy may be due to the inability of commonly used growth models to reconcile such rapid juvenile growth with the slow growth predicted for subadults and adult sharks. Direct age-validation techniques, such as oxytetracycline (OTC) marking and recapture of an adequate sample size of Shortfin Mako ≤ 200 cm FL, therefore, are needed to help resolve the issue of band-deposition rates in juvenile Shortfin Mako vertebrae.

In this study, we examined OTC-marked vertebrae of 29 juvenile Shortfin Mako (≤ 200 cm FL) released off California and later recaptured from 2000 to 2010 (at liberty from 145 days to 4.4 years). OTC is deposited at sites of active calcification, such as vertebral centra, and is known to remain distinct for at least 20 years in certain finfish, such as the Sablefish (*Anoplopoma fimbria*) (Beamish and McFarlane, 2000), and sharks, such as the Leopard Shark (*Triakis semifasciata*) (Smith et al., 2003). The combination of tag-recapture and chemical marking is thought to be the most robust method of age validation (Campana, 2001; Goldman, 2005). These methods test the accuracy of the counts of vertebral band pairs as annual indicators through observation of the banding pattern deposited distally to the OTC mark during the known time at liberty. To supplement this information, we also conducted analyses of at-liberty growth of tagged-recaptured sharks and length-

frequency data from 3 decades of length data from commercial and research sources.

Materials and methods

Tagging methods

Sharks for tagging and OTC injection were captured in the Southern California Bight (SCB) (Fig. 1) with baited pelagic longlines and identified as Shortfin Mako through the method described by Compagno (2001). Leaders were unsnapped from the main line, and sharks were guided into a semisubmerged metal tagging cradle at the stern of the vessel. The cradle was then raised to facilitate tagging, measuring, and OTC injection, while the eyes of the shark were covered with a wet chamois cloth and a saltwater ventilation hose continuously ran water over the shark's gills. Each shark was tagged on the dorsal fin with a plastic Rototag² (Dalton ID, Henley-on-Thames, UK) labeled with contact and reward information in English and Spanish and with instructions to measure the fish and save the vertebrae. Most sharks also were double-tagged with a spaghetti tag placed in the dorsal musculature beneath the first dorsal fin.

At tagging, the sex of each shark was determined and each shark was measured (straight line FL or total length [TL]) to the nearest centimeter with a stationary meter stick fitted to the shark tagging cradle. Sharks were given an intraperitoneal injection of OTC at a dose rate of 25 mg/kg of body weight; the dose was estimated with a length-weight dose table developed from length-weight measurements of Shortfin Mako measured by NOAA scientific observers for the California drift gillnet fishery (Rasmussen³).

Laboratory methods for processing vertebrae

Past studies have shown that band counts are consistent throughout the vertebral column in the Shortfin Mako, indicating that vertebrae from any region can be used in age analysis, although the larger central vertebrae are easier to read because of wider band spacing (Bishop et al.¹; Bishop et al., 2006; Natanson et al., 2006). OTC-marked vertebrae were obtained from Shortfin Mako recaptured on research cruises and commercial and recreational fishing vessels between 2000 and 2010. The widest diameter vertebral centra in a given sample were chosen for sectioning. We used only OTC-marked vertebrae from tag recaptures at liberty longer than 124 days (or ~4 months) to incorporate one full season into band-pair counts.

² Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

³ Rasmussen, R. 1995. Unpubl. data. Southwest Fisheries Science Center, NOAA, La Jolla, CA.

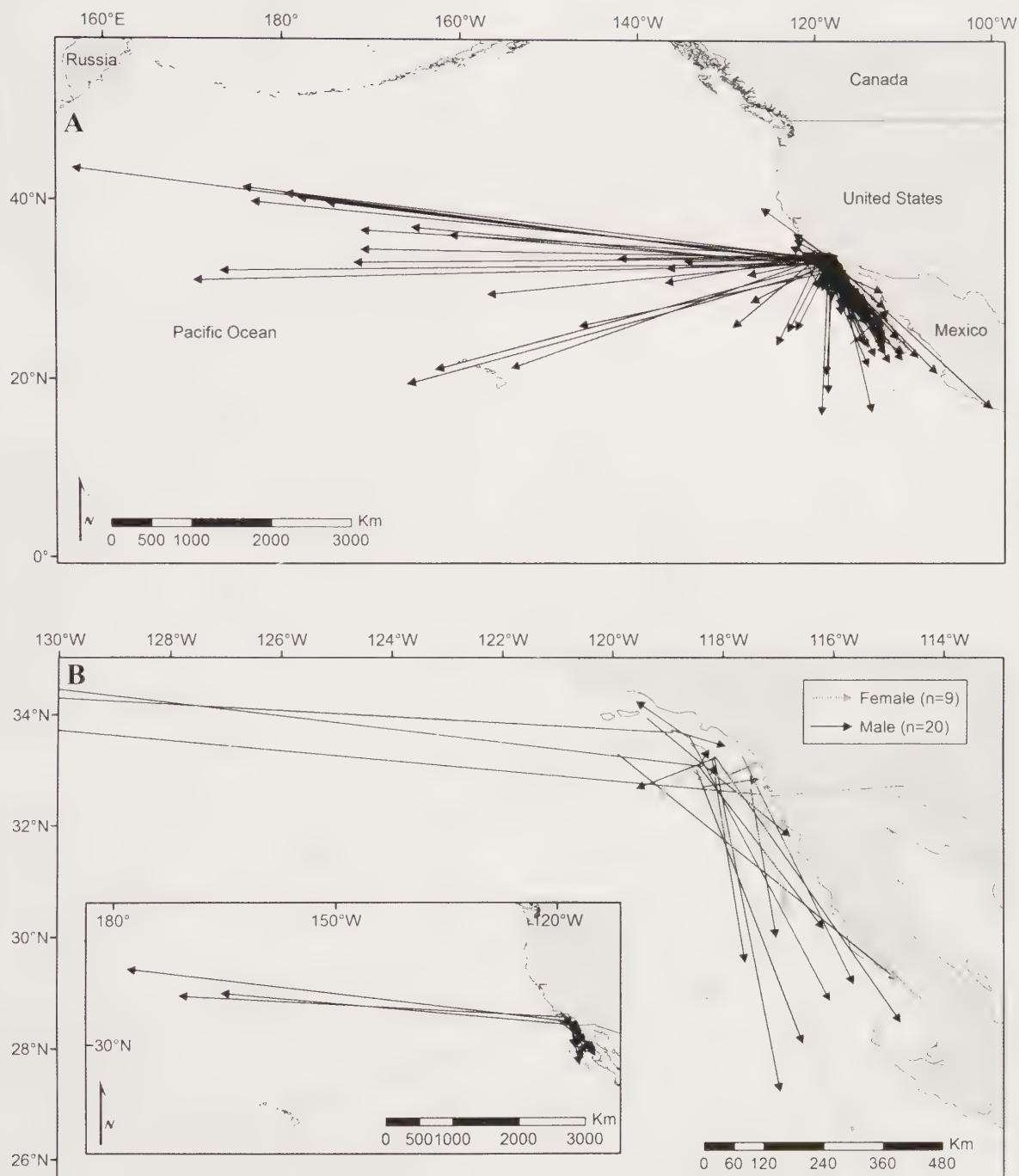


Figure 1

Map of study area in the Southern California Bight with tag and recapture locations (triangles) for (A) all recaptured Shortfin Mako (*Isurus oxyrinchus*) (OTC-marked and unmarked ($n=317$)) and (B) recaptured OTC-injected juvenile Shortfin Mako ($n=29$) during the study period from 1996 to 2010. In panel B, black and gray arrows represent males and females, respectively, and the inset shows the more distant recapture locations.

To elucidate the vertebral bands, we chose to duplicate the “hard” (high-frequency) X-radiography technique of Cailliet and Bedford (1983) and Cailliet et al. (1983), which was used in the only cen-

trum aging study of Shortfin Mako off California to date. This type of high-resolution radiography, with industrial, fine-grain, high-contrast film for sharpness and sensitivity, operates in the range of

10–110 kV at 3 mA and penetrates the highly calcified vertebrae.

Samples were stored frozen until processed and kept from light and excessive UV exposure to preserve the OTC time mark. Whole centra were separated, cleaned of excess tissue, rinsed and air-dried. Once dry, 2 centra from each sample were chosen, and 2 types of sections were prepared with a low-speed circular saw (IsoMet, Buehler, Lake Bluff, IL). To duplicate the Cailliet et al. (1983) method of X-raying the whole centrum face and to avoid the double image of the anterior and posterior face superimposed in X-ray images, a transverse cut was made through the centrum to create 2 equal halves of the centrum face. Additionally, longitudinal (sagittal) sections, 0.3–1.0 mm thick, were taken from the center of the second vertebrae to further elucidate banding patterns, especially growth zones along the centrum edge that are sometimes difficult to read on centrum face X-rays (Cailliet et al., 1983). Sections were then mounted and examined under a dissecting microscope at 7.5–10.0 $\times$ magnification, with reflected long-wave UV light (365 nm) to illuminate the OTC mark. A metal pin was glued into place to visualize the position of the brightest, most distal edge of the OTC mark before it was X-rayed. Samples were X-rayed with a General Electric (Fairfield, CT) Mobile 100-15 X-ray unit for exposures between 15 and 45 s at 5 mA and 20–40 kV by using Kodak Industrex M100 film (Readypack II; Eastman Kodak Co., Rochester, NY). X-radiographs were photographed with a Leica Z16 APO dissecting microscope with substage illumination and a Leica DFC420 digital camera (Leica Microsystems, Wetzlar, Germany).

Standardization of band-reading techniques and terminology

We examined data collected by commercial drift gill-net observers and from research longline surveys and determined the peak in abundance of postpartum-size Shortfin Mako <70 cm FL to identify peak parturition time off southern California. Most individuals (90%) were collected between August and November, providing a tentative parturition time in our study region. Size at birth has been estimated at approximately 63 cm FL (70 cm TL), with parturition occurring year-round according to Mollet et al. (2000); parturition may occur primarily in summer in the South Pacific (Duffy and Francis, 2001) and eastern North Atlantic (Maia et al., 2007). The birth band for counting purposes was identified as the most pronounced calcified first band distal to the centrum focus and indicated by a change in the angle of the centra (Bishop et al., 2006). Seasons were defined according to solstice and equinox periods in the Northern Hemisphere.

Band-pair counts

Band pairs were counted from digital images of X-ray photographs on a computer screen. We referred to the

original X-rays if more detail was desired. As in Bishop et al.¹ and Bishop et al. (2006), counts excluded the birth band, which represents age 0. Alternating pairs of translucent bands (hypomineralized; appearing dark in X-ray) and opaque bands (hypermineralized; appearing light in X-ray) were assumed to represent one complete band pair. Two separate band counts were made: 1) total band pairs, or bands distal to the presumed birth band, and 2) band pairs distal to the OTC mark. Band-pair counting began for the former at the distal edge of the first translucent zone beyond the birth band and for the latter at the distal edge of the first translucent zone beyond the OTC mark. In many cases, the OTC mark was directly on a translucent zone, but this zone was not included in the distal-to-OTC counts because only partial growth occurred during this period. This method results in counts that are conservative; counts are lower than they would be if this zone were included. If a count ended with a partial band pair (observed when the centrum edge was opaque), a plus sign was appended to the count number. For statistical analyses, the plus sign was converted to an arbitrary partial band count of 0.5. The corpus calcareum (centrum “arm”) was used as a primary counting surface, and bands in the intermedialia were used for confirmation of a band pair, although we were not always successful in acquisition of sections with the fragile intermedialia intact (Goldman, 2005; Branstetter and Musick, 1994).

Each sample was examined and counted independently by 3 readers. Bands were “blind” counted without knowledge of Shortfin Mako length, sex, or time at liberty. Readers consulted with each other on criteria for counts before readings. Samples for which there was disagreement were counted a second time with X-ray images from which corresponding sample numbers had been removed and placed in a random order. Counts with similar readings among readers were deemed final; however, several samples did not have similar counts. For those samples without similar counts, the average number of band pairs was reported because differences were minor and no readings were deemed irreconcilable.

Differences among final readings of each of the 3 independent readers were examined through an analysis of variance (ANOVA) with readers as the dependent variable. A least-squares linear regression analysis was performed, and the null hypothesis that the slope (*b*) of the relationship between the number of band pairs and time was 1:1 (a situation that occurred if one opaque and one translucent band were deposited each year) was tested with a two-tailed *t*-test (Kusher et al., 1992). Age bias was investigated with age-bias plots and chi-square tests of symmetry by using the contingency table methods of Bowker (1948) and Hoenig et al. (1995). Differences in band-pair counts among readers were evaluated by the average percent error (APE) (Beamish and Fournier, 1981) and coefficient of variation (CV) (Chang, 1982) for readings distal to both the OTC mark and birth band.

Length-frequency analysis

Length-frequency distributions of juvenile Shortfin Mako were analyzed to estimate size at age of the first 3 age classes and to compare to vertebrae readings. The MULTIFAN model (Fournier et al., 1990) was one of 2 techniques used to analyze length-frequency data on the basis of size distributions. This model simultaneously analyzes multiple length-frequency distributions using a maximum likelihood method to estimate the number of age classes and proportions of fish at age. Tests for significance (best-fit growth parameters) were made through the use of likelihood ratio tests. First, a systematic search was performed to estimate the number of age classes and to hold the standard deviations of length constant across all age classes. Next, standard deviations of length were allowed to vary across age classes. The MIXDIST package (MacDonald and Pitcher, 1979) in R, vers. 2.8.0 (R Development Core Team, 2008) was the second length-frequency analysis used. This analysis uses a maximum likelihood method to estimate proportions of fish at age with the added benefit of fitting non-normally distributed data.

Data for both techniques were analyzed annually and came from 2 sources: 1) fishery-dependent data from the California drift gillnet fishery (1981–2009), which operates between May and January, and 2) fishery-independent data from longline research surveys of juvenile Shortfin Mako conducted by the NOAA Southwest Fisheries Science Center (1993–2009) between June and August of each year. A mixture of length measurements taken across study years: TL, FL and alternate length (AL, straight line distance between the origins of the first and second dorsal fins) were standardized into FL for this study to allow for comparison of our results with the results of other studies. The following length conversions were obtained from the 2 sources and used to standardize data for subsequent length-frequency analyses:

$$FL = 0.913 \times (TL) - 0.397, \text{ coefficient of determination } (r^2) = 0.986 \text{ } (n=2177)$$

$$FL = 2.402 \times (AL) + 9.996, r^2=0.957 \text{ } (n=3250).$$

Size data were combined between sexes because no significant difference existed ($P=0.769$), and size bins of 5 cm, ranging from 55 to 265 cm FL, were used.

Growth of tagged and recaptured mako sharks

Growth rates were calculated for 1) recaptured, OTC-marked sharks and 2) angler- and research-released, unlabeled sharks for which reliable length estimates were available ($n=62$ of 317 returns) (Fig. 1A). Growth was estimated with the tag-recapture growth model GROTAG (Francis 1988a, 1988b) on the basis of length and time-at-liberty. This model was chosen because age-based and length-based growth models often differ, and it is a useful alternative for comparison of

growth rates at particular sizes (Francis, 1988a; Natanson et al., 2006; Claisse et al., 2009). We used a maximum likelihood approach with this model to estimate growth rates (g_α and g_β) at 2 selected lengths (α and β), a CV of growth variability, mean measurement error and standard deviation, and outlier probability. Therefore, estimated growth of a Shortfin Mako, i , was calculated with the following equation:

$$\Delta L_i = ((\beta g_\alpha - \alpha g_\beta) / (g_\alpha - g_\beta) - L_i) / (1 - (1 + (g_\alpha - g_\beta) / (\alpha - \beta))^{\Delta T_i}),$$

where L_i = length at release; and

ΔT_i = the tag deployment time.

Results

Tagging and recapturing oxytetracycline-marked sharks

Off southern California from 1996 to 2010, 940 OTC-injected Shortfin Mako were tagged and released (Fig. 1, A and B). Of the subset of released sharks for which sexes were determined, 67% were males and 33% were females. Average size at release was 110 cm FL (± 0.80 SE). Of the released OTC-marked sharks, 35 were recaptured from 2000 to 2010. Of these 35 sharks, 29 fish were selected for this study because they had been at liberty for ≥ 4 months and OTC marks in the vertebrae fluoresced (Table 1, Fig. 1B). Five samples were excluded from analysis because of a short time-at-liberty (within a range from 24 to 60 days), provided no information on band-pair progression, and in the case of 1 shark, the vertebrae did not fluoresce.

For the 29 fish used in this study, average time-at-liberty was 522 days (± 71.0 SE), within a range from 145 to 1594 days, and average size was 109 cm FL (± 2.9 SE) at tagging and 148 cm FL (± 5.0 SE) at recapture (Table 1). The average displacement distance (great-circle distance from tagging to recapture location) for the 29 OTC-marked Shortfin Mako was 902 km (± 291 km SE), within a range from 2 to 5295 km (Fig. 1B). According to results from analyses with linear regressions, no significant effects of time-at-liberty or size-at-tagging existed in relation to total displacement distance ($P>0.05$).

Age validation results

Results from readings of the OTC-marked vertebrae indicated that 2 band pairs are deposited each year in samples analyzed in this study. The observed slope of the relationship between the number of band pairs each year and years-at-liberty significantly differed from the 1:1 relationship ($P<0.01$). Specifically, the average number of band pairs predicted each year was modeled with the following linear regression: average number of band pairs = $1.988 \times (\text{number of years-at-large}) - 0.136$, $r^2=0.942$ ($P<0.05$) (Fig. 2).

Table 1

Summary table of OTC-marked vertebrae samples from juvenile Shortfin Mako (*Isurus oxyrinchus*) recaptured from 2000 to 2010 in the Southern California Bight for this study. Samples are sorted by time at liberty, and information includes tag and recapture dates and fish lengths and sex. The average number of band pairs (from 3 independent readers) is provided for after the OTC mark and birth band mark (± 1 standard error [SE]). NL=either no length estimate or an unreliable one. *=fork length (FL) was converted from total length or alternate length (first dorsal to second dorsal fin).

Fish ID	Time at liberty (days)	Tagging date	Recapture date	Tagging length (cm FL)	Recapture length (cm FL)	Sex	Average number of band pairs after OTC mark (± 1 SE)	Average number of band pairs after birth band mark (± 1 SE)
A037789	1594	7/11/2000	11/21/2004	108	200	F	7.3 (0.9)	9.3 (0.7)
A037559	1512	6/21/2001	8/11/2005	110*	190*	M	8.7 (0.3)	11.7 (0.3)
A038423	1198	7/9/2005	10/19/2008	91	157*	M	7.8 (0.6)	11.5 (0.3)
A037655	1133	7/06/2001	8/12/2004	89*	157*	F	5.3 (0.2)	8.2 (0.2)
A038734	836	7/5/2004	10/19/2006	106*	172*	M	5.0 (0.0)	9.0 (0.0)
A038611	733	6/19/2004	6/22/2006	111*	152	F	4.0 (0.0)	6.0 (0.0)
A039992	730	7/28/2007	7/27/2009	92	146	M	4.0 (0.0)	6.0 (0.0)
A039946	555	8/1/2007	2/6/2009	109	150	M	2.5 (0.0)	4.5 (0.0)
A038623	531	6/22/2004	12/05/2005	130*	154	M	2.3 (0.2)	7.3 (0.2)
A058923	463	6/30/2002	10/06/2003	108*	139*	M	2.5 (0.0)	5.2 (0.7)
A058969	446	6/23/2003	9/11/2004	98*	125*	M	2.3 (0.2)	4.7 (0.4)
A040354	407	8/13/2009	9/24/2010	98	137*	M	2.3 (0.2)	3.8 (0.2)
A039341	400	7/24/2007	8/27/2008	131	160*	M	1.5 (0.0)	5.5 (0.0)
A058916	382	7/01/2002	7/18/2003	137*	162*	F	1.5 (0.0)	4.5 (0.0)
A038924	373	7/21/2005	7/29/2006	129	163*	M	2.0 (0.0)	5.5 (0.3)
A039374	364	7/15/2007	7/13/2008	129	154	M	2.0 (0.0)	7.0 (0.0)
A038091	350	6/24/2005	6/9/2006	128	135	M	2.0 (0.0)	7.5 (0.3)
A038404	335	7/8/2005	6/8/2006	117	NL	M	1.5 (0.0)	5.0 (0.3)
A040327	323	8/11/2009	6/30/2010	96	114*	M	2.0 (0.0)	5.0 (0.6)
A038589	313	8/14/2004	6/23/2005	124	141*	M	1.5 (0.0)	7.5 (0.6)
A040251	298	8/4/2009	5/29/2010	105	141*	F	1.0 (0.0)	3.3 (0.3)
A040374	298	8/15/2009	6/9/2010	100	NL	F	1.2 (0.2)	3.2 (0.2)
A040302	277	8/8/2009	5/12/2010	89	103	M	1.2 (0.2)	3.5 (0.3)
A039912	270	8/2/2007	4/28/2008	79	98	F	2.3 (0.2)	3.3 (0.2)
A040788	253	8/23/2009	5/3/2010	124	164*	M	0.8 (0.2)	5.3 (0.2)
A038854	211	7/29/2009	2/25/2010	108	NL	F	0.8 (0.2)	2.7 (0.2)
A039669	206	6/14/2008	1/6/2009	92	NL	M	1.0 (0.0)	3.0 (0.0)
A040798	193	8/24/2009	3/5/2010	122	NL	F	1.0 (0.0)	4.3 (0.2)
A038445	145	7/10/2005	12/2/2005	88	NL	M	1.0 (0.0)	3.3 (0.3)

Results of the vertebral centrum analysis are summarized in Table 1, including time at liberty, average number of band pairs observed distal to the OTC mark, and average number of band pairs observed distal to the birth band. In addition, Figure 3 shows banding patterns and band-pair counts for 5 vertebrae from Shortfin Mako at liberty from 206 to 1512 days.

Visual band-pair counts (identified by arrows in Fig. 3) were agreed upon post hoc by all 3 readers, and 3 samples had full agreement among readers during independent readings; however, 2 samples did not have complete agreement during independent readings. Band-pair counts distal to the OTC mark for sample A037559 were 9, 9, and 8, and distal counts to the birth band were 12, 12, and 11. Sample A039912 had band-pair counts of 2.5, 2.5, and 2

distal to the OTC mark and 3.5, 3.5, and 3 distal to the birth band.

All tagging activities occurred during summer months when translucent zones appeared in the vertebrae (Fig. 3). In contrast, both translucent and opaque zones were found at the outer edge of vertebrae for samples collected throughout the year without any apparent seasonal patterns.

There were no significant differences among band-pair counts distal to the OTC mark (ANOVA; $P=0.978$) or among total counts distal to the birth band (ANOVA; $P=0.955$). Age bias was negligible: age-bias plots (Fig. 4) and chi-square tests of symmetry showed no systematic bias ($P>0.05$), confirming that differences were due to random error. Variability among reader counts was low with an APE of 4.36% and CV of 5.71% for counts

distal to the OTC mark and with an APE of 5.65% and CV of 7.73% for counts distal to the birth band. Among readers, 93% (27 of 29) of the final band-pair estimates distal to the OTC were within 1 band pair of each other, and 86% (25 of 29) of the estimates distal to the birth band were within 1 band pair.

The readings distal to the OTC that differed by more than one band pair were from sharks that had been at liberty for the longest time, indicating that variability in band-pair counts increases with age, likely because of disagreement among readers caused by structural artifacts. For example, sample A037789 was from a shark that was at liberty for 1594 days and band-pair estimates distal to the OTC varied from 6 to 9 among the 3 readers for this shark (Table 1).

Length-frequency analysis

A total of 14,720 individual Shortfin Mako were used for the length-frequency analysis that was completed with fishery-dependent data from the California drift gillnet fishery (1981–2009) and fishery-independent data from juvenile Shortfin Mako surveys (1993–2009) (Fig. 5). No differences in length-frequency modes were detected when analyzed by season or sex; therefore, parameter estimates were generated by grouping across factors (season and sex) with age-dependent standard deviation incorporated into the model. Average size of Shortfin Mako used in growth modeling was 121.3 cm FL (± 0.25 SE). The majority of fish (85%) ranged in size from 80 to 160 cm FL with 3 identifiable modes consistently present in annual length frequencies regardless of survey type or sex.

Results from MULTIFAN showed these 3 modes at 86, 112, and 134 cm FL, and average modal sizes from MIXDIST were 83, 118, and 147 cm FL. Taking the difference between modal sizes from MULTIFAN analysis provided average annual growth rates of 27 and 23 cm FL for the period from the first to second mode and for the period from the second to third modes, respectively (Table 2). Similarly, annual growth rates from MIXDIST averaged 36 and 29 cm FL for the same 2 periods (Table 2).

Growth of tagged and recaptured sharks

No difference was observed between growth rates calculated from at-liberty OTC-injected sharks (28 and 21 cm per year at 85 and 130 cm FL, respectively) and tag-recaptured sharks not injected (29 and 19 cm per year at 85 and 130 cm FL, respectively); therefore, these data were pooled. The growth rates that resulted from GROTAG analysis of lengths of tagged and recaptured sharks were similar to the growth rates from length-frequency calculations, averaging 29

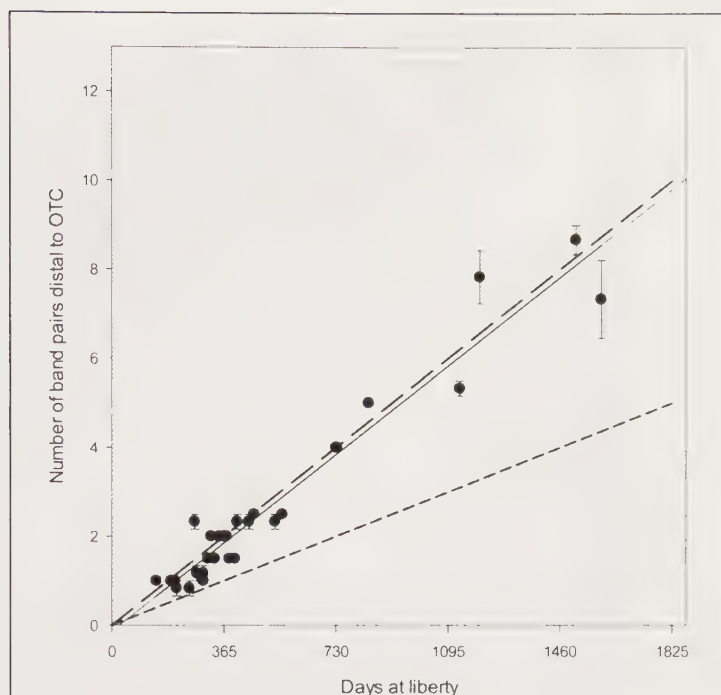


Figure 2

Average number of band-pairs (translucent and opaque) for the number of days at liberty, determined from the oxytetracycline (OTC) mark to the outer centrum edge on vertebrae of juvenile Shortfin Mako (*Isurus oxyrinchus*) ($n=29$) tagged from 2000 to 2010 in the Southern California Bight for this study. Readings were based on 3 independent readers (± 1 standard error [SE]). The solid line shows the linear regression of number of band pairs relative to days at liberty, and the lines with short and long dashes show predicted number of band pairs for 1 band pair/year and 2 band pairs/year, respectively.

and 20 cm per year at 85 and 130 cm FL, respectively (Table 2).

Discussion

Results of this study indicate that 2 band pairs are deposited each year in juvenile Shortfin Mako tagged and released in southern California. The fast growth rates collectively obtained through the use of OTC-marked vertebrae, MULTIFAN and MIXDIST length-frequency analyses, and tag-recapture growth models were consistent, providing strength to our results beyond the usefulness possible with the employment of a single method alone. Further, a sample size of 29 OTC-marked vertebrae of Shortfin Mako at liberty from 4 months to more than 4 years is the most comprehensive OTC tag-return data set reported for this species. We also compared our total band-pair counts at length with those of Cailliet et al. (1983), the only other Shortfin Mako age and growth study completed

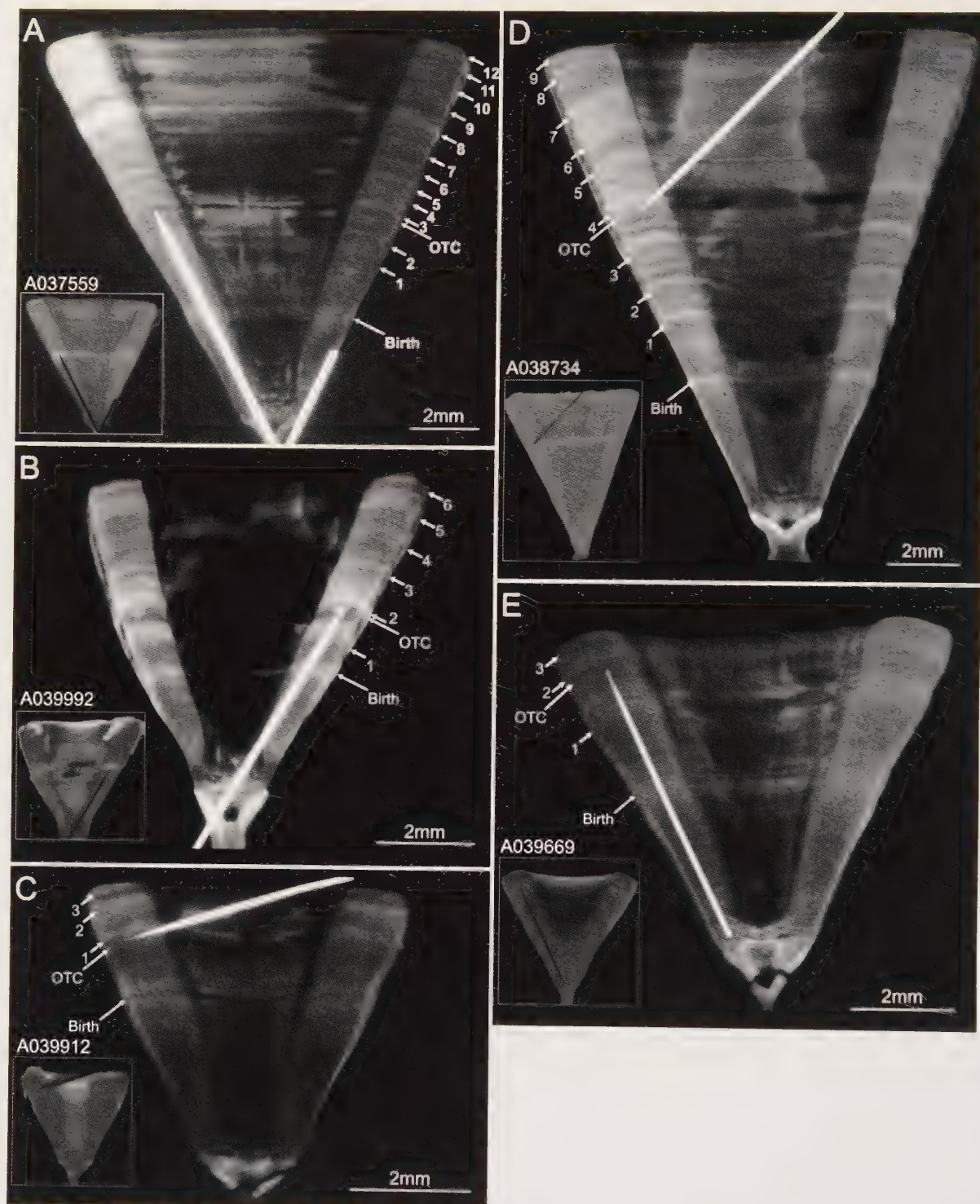


Figure 3

X-ray images of vertebrae sections that show band-pair progression of 5 OTC-marked juvenile Shortfin Mako (*Isurus oxyrinchus*) recaptured during this study off southern California. The small inset in each image shows the OTC fluorescence under UV light. Translucent or hyaline (rapid growth) bands or darker areas of vertebrae show periods of rapid growth, and opaque bands or lighter areas of vertebrae show periods of slow growth. Arrows indicate band-pair counts.

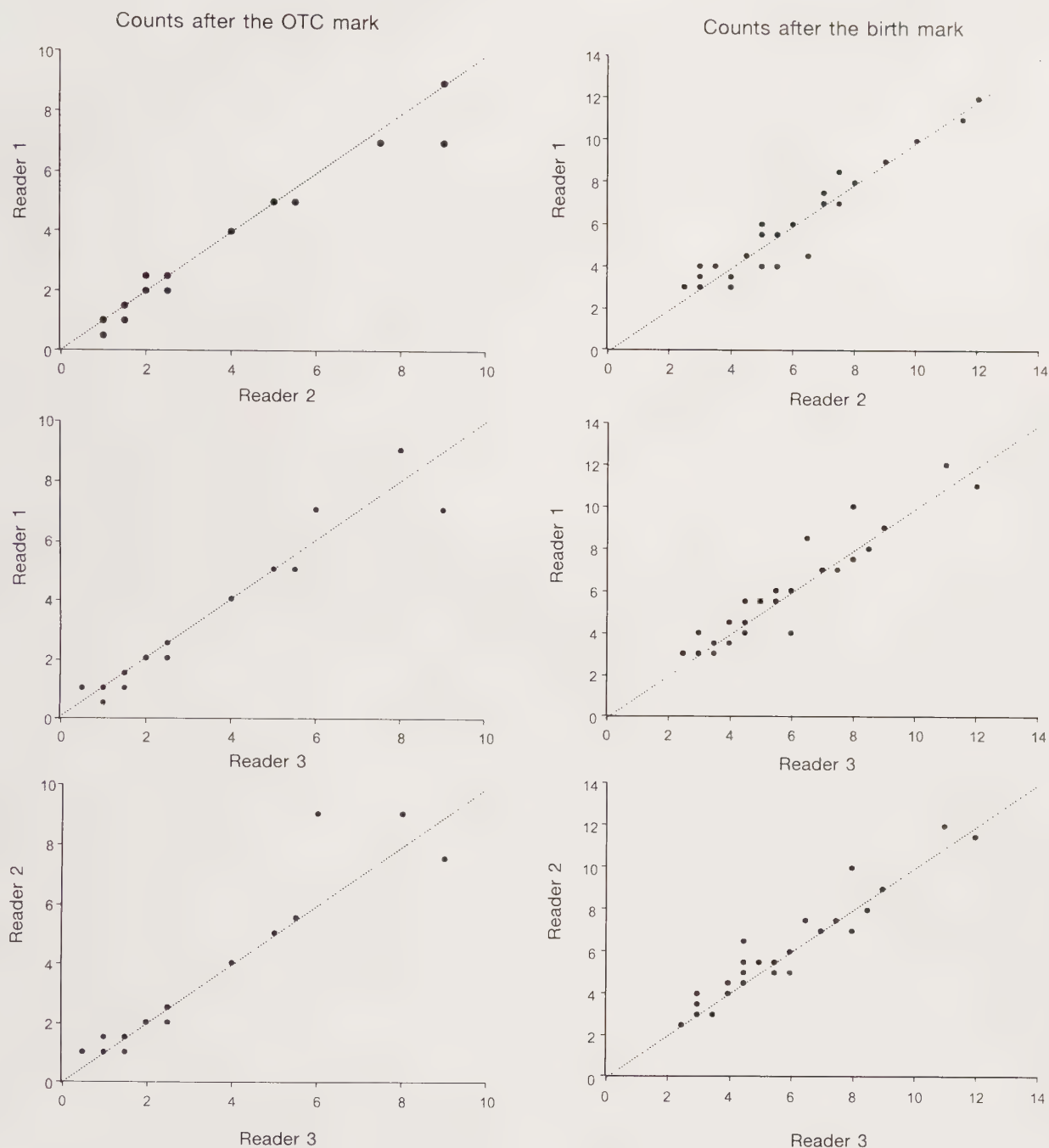


Figure 4

Age-bias plots for all OTC-marked juvenile Shortfin Mako (*Isurus oxyrinchus*) independently aged by 3 readers during this study. Graphs in the left column represent total band-pair counts distal to the OTC mark, and graphs in the right column represent total band-pair counts distal to the birth band.

in this region, to determine if vertebral readings or assumptions about growth-band deposition differed. Total band-pair counts relative to fish size in this study were very similar to the average band-pair counts, relative to fish size, obtained by Cailliet et al. (1983) (Fig. 6).

This finding indicates that vertebral readings were similar between the 2 studies and only the assumption about deposition rates differed.

Given differences in the rates of band-pair deposition of Shortfin Mako in other studies, our findings

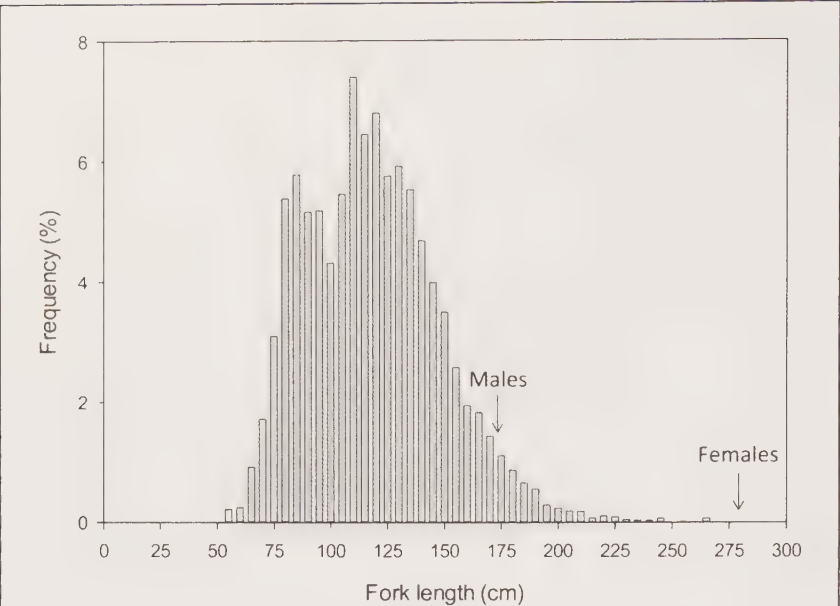


Figure 5

Total percent length-frequency distribution of Shortfin Mako (*Isurus oxyrinchus*) collected from fishery-dependent (1981–2009) and fishery-independent (1993–2009) surveys conducted in the Southern California Bight. Vertical bars are placed in length bins of 5 cm along the x-axis, showing the range of fork lengths (FL) from 55 to 265 cm FL. Arrows show the approximate size at 50% maturity for males and females determined by Semba et al. (2011).

should not be extrapolated beyond our size range and geographic area; however, our results indicate that growth patterns of juvenile and adult Shortfin Mako merit additional research.

The differences in rates of band-pair deposition of Shortfin Mako among studies may be due to a number of factors, including study location, methods, and ontogeny. Rates of band-pair deposition of the Common Carp (*Cyprinus carpio*) vary geographically among sim-

ilar age classes of the same species; biannual deposition occurs in South Africa (Winker et al., 2010) and annual deposition occurs in Australia (Brown et al., 2004), exemplifying the importance of regional age validation.

In one of the first Shortfin Mako aging studies, Pratt and Casey (1983) read silver-nitrate-stained, whole vertebral centra collected in the north-west Atlantic and suggested that 2 band pairs were deposited annually, after noting that calculated growth under this assumption closely matched direct observations of growth over time for this species (especially for fish ≤ 200 cm FL). Pratt and Casey’s (1983) growth curves were generated from tag-recapture growth data collected in the field, temporal analysis of length-month information, and a vertebral age-based growth curve corroborated and compared with length-frequency mode analyses.

In contrast, Cailliet and Bedford (1983) and Cailliet et al. (1983) used hard (high-frequency) X-radiography and silver nitrate staining of whole centra to elucidate banding patterns of Shortfin Mako in the northeast Pacific. The authors of both studies assumed that only 1 band pair was

deposited annually and obtained a growth rate of about half the rate of that of Pratt and Casey (1983), but they did not test the assumption of 1 versus 2 band pairs per year.

Campana et al. (2002) concluded that the hypothesis of a single band pair was the most consistent with the banding pattern obtained from a 21-year-old Shortfin Mako (328 cm FL) collected from the northeast Atlantic and aged with bomb-radiocarbon techniques. Ardizzone

Table 2

Estimates from the tag-recapture growth model with GROTAG for juvenile Shortfin Mako (*Isurus oxyrinchus*) in the eastern Pacific ($n=62$). Growth estimates from the length-frequency techniques (MULTIFAN and MIXDIST) also are included for the first 2 age classes. K =Brody growth parameter, L_{∞} =mean asymptotic length.

Parameter	Symbol (unit)	Tag-recapture growth model	Length frequency (MULTIFAN)	Length frequency (MIXDIST)
Growth rate	g_{85} (cm/year)	29	27	36
	g_{130} (cm/year)	20	23	29
K	(per year)	0.19	0.17	
L_{∞}	(cm)	231.03	252.12	
Growth variability	v	0.31		
Mean measurement error	m (cm)	2.87		
Standard deviation measurement error	s	4.46		
Log likelihood	λ	-235.8		

et al. (2006) expanded on this study with 54 samples used for radiocarbon chronologies. Their results supported the hypothesis of annual band-pair deposition for older ages, but they did not rule out biannual band-pair deposition for young fish. Similarly, Natanson et al. (2006) reiterated the aforementioned results and presented evidence of annual band-pair formation from an OTC-injected, 241-cm-FL, male Shortfin Mako at liberty for just over 1 year. However, growth curves generated from their tag-recapture and length-frequency data showed a much faster growth rate for young Shortfin Mako than the rate calculated from vertebrae data, and the authors suggested the possibility that rates of band deposition may change with ontogeny.

Bishop et al.¹ and Bishop et al. (2006) examined age and growth of Shortfin Mako from New Zealand waters and assumed a deposition rate of 1 band pair per year on the basis of Campana et al. (2002) and Ribot-Carballal et al. (2005). They obtained a growth curve similar to that of Cailliet et al. (1983), and their best-fit Schnute growth model predicted that growth was fast for the first few years of life (39 cm during year 1), then slowed for older ages to a rate that is similar to juvenile growth rates found in our study. Like Pratt and Casey (1983), they found that length-frequency data indicated considerably faster growth than did estimates from vertebral ages for the younger age classes with the assumption of 1 band pair per year. Through the use of cohort analysis, Maia et al. (2007) also reported fast growth in juvenile Shortfin Mako collected from the longline fishery in the eastern North Atlantic (average growth rate of 61.1 cm/year for the first year, and 40.6 cm/year for the second year).

More recently, Okamura and Semba (2009) and Semba et al. (2009) examined monthly centrum edge patterns with a new statistical method and surface shadow technique to determine periodicity of band-pair formation. Their results indicated that the deposition of band pairs in Shortfin Mako in the western and central North Pacific has an annual cycle, but they also warned about sources of error from inaccuracies in centrum margin readings and from a large variability in the timing and duration of band deposition.

Biannual band-pair deposition is not species-specific to Shortfin Mako; it reportedly has occurred in other shark species as well. Chen et al. (1990) and Anislado-Tolentino et al. (2008) suggested biannual band-pair deposition in the Scalloped Hammerhead (*Sphyrna*

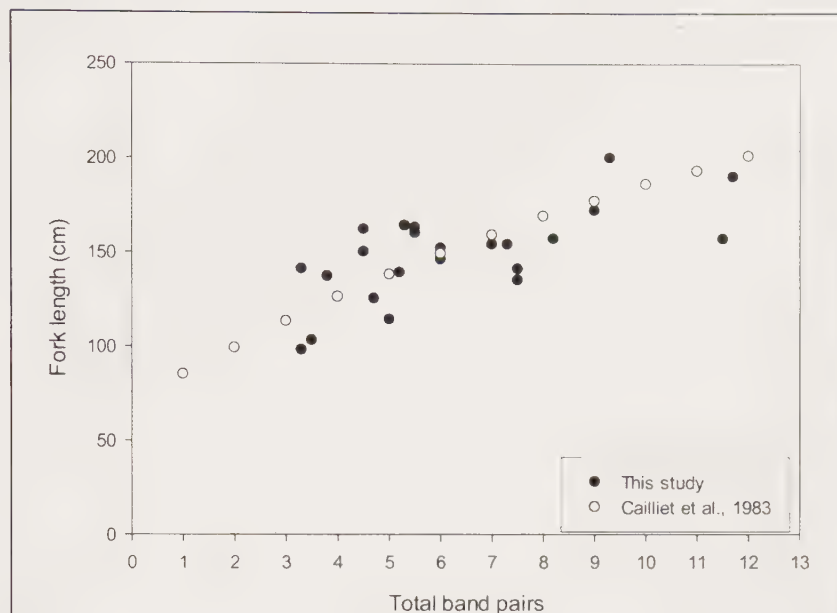


Figure 6

Individual band-pair counts relative to size, shown in fork length (cm), of juvenile Shortfin Mako (*Isurus oxyrinchus*) from this study ($n=29$) compared with the average number of band-pair counts relative to size by Cailliet et al. (1983). Vertebral readings were similar between these 2 studies, and only the assumption about deposition rates differed. Sharks for both studies were captured off southern California.

lewini). In addition, Parker and Stott (1965) suggested that 2 band pairs were laid down annually in the Basking Shark (*Cetorhinus maximus*); however, those conclusions were questioned by Pauly⁴ (2002). Further, Natanson et al. (2008) examined vertebral growth patterns in *C. maximus* as a function of ontogeny and questioned the feasibility of aging this species with vertebral band-pair counts.

Ontogenetic differences may play a critical role in band-pair formation for Shortfin Mako, as well. Unfortunately, none of our OTC-marked vertebrae were from sharks >200 cm FL at tagging or recapture, but the 3 largest sharks at recapture (172, 190, and 200 cm FL) exhibited a pattern consistent with biannual deposition. Two of these sharks (200 and 190 cm FL) were at liberty for more than 4 years and averaged 7.3 and 8.7 band pairs distal to the OTC mark, respectively, indicating that the biannual pattern continues in fish of this size. Both had similar total band-pair counts, averaging 9.3 and 11.7, respectively.

If one assumes a biannual pattern, as indicated by our OTC marking results, these fish would range from

⁴ Pauly, D. 1978. A critique of some literature data on the growth, reproduction and mortality of the lamnid shark, *Cetorhinus maximus* (Gunnerus). ICES Council Meeting Doc. 1978/H:17, 10 p.

4.5 to 6 years of age when collected. Examination of vertebral centra from some of our larger, non-OTC-tagged, recaptured Shortfin Mako reveals that as fish approach maturity, banding patterns appear to become more distinct, with both fast and slow growth zones becoming more regular and evenly spaced. Therefore, it is possible that these larger fish, on entering a more oceanic realm, change the periodicity of their banding pattern. On the basis of these results, it appears that Shortfin Mako ≤ 200 cm FL and found off California grow much faster than previously thought, with observed rapid growth (biannual band deposition) for approximately the first 6 years of life. Slower growth (annual deposition) thereafter may occur but cannot be confirmed by this study.

Mechanisms that drive the observed biannual band-pair deposition may be linked to seasonal migration patterns and subsequent food availability. Through the use of similar OTC tag-recapture methods, Murphy et al. (1998) determined that Black Drum (*Pogonias cromis*) begin to deposit biannual band pairs after 4 years of age because of a shift in migration patterns. Similarly, Shortfin Mako tagged in southern California appear to exhibit a biannual growth cycle, with fast-growth periods (wide, translucent band formation) in summer and winter and slow-growth periods (narrow, opaque band formation) in spring and fall. One possible explanation is that, as coastal waters warm and cool seasonally, juvenile Shortfin Mako move between rich feeding grounds off California in the summer and off Mexico in the winter and spend spring and fall migrating between these feeding areas.

Of the 15 OTC-marked sharks recaptured in Baja Mexico waters (Fig. 1B), only 2 sharks were recaptured during summer months. In contrast, 70% of the returns of OTC-marked sharks in California coastal waters occurred during summer and there were no returns in the winter. In addition, on the basis of data from all tag recaptures (OTC and non-OTC-marked sharks, $n=317$, senior author, unpubl. data), 40% of all shark recaptures in Mexico (south of 30°N) occurred during winter, but only 7% of sharks were recaptured in Mexico during summer. Likewise, 58% and 7% of all recaptures in California coastal waters occurred during summer and winter seasons, respectively. Preliminary analysis of movements of juvenile (<150 cm FL) Shortfin Mako tracked with satellite tags (2003–10, $n=26$) also shows high relative densities of Shortfin Mako at reported locations off Baja California, Mexico, in the winter and off California in the summer and more dispersive offshore movements in the spring and fall (S. Kohin, unpubl. data).

Tag-recapture techniques with OTC are among the most powerful methods for validation of age and growth patterns in fishes, but there are difficulties with this method. One disadvantage in the use of chemical marking and recaptures is that the number of band pairs formed for short times between tagging and recapture is often low, resulting in a potentially large

relative error if one of the band pairs (such as on the growing edge) is misinterpreted (Campana, 2001). For example, misinterpretation of a single growth zone in a fish at liberty for 2 years would result in a 50% error, but the same misinterpretation in a fish at liberty for 10 years would produce an error of only 10%. Fortunately, the relatively large sample size of 15 sharks at liberty for more than 1 year and 4 sharks at liberty for more than 3 years (2 of them for more than 4 years) allowed us to confirm the consistent banding patterns between both short- and long-term deployments.

An additional problem with the use of chemical marking techniques, such as with OTC, is that growth may be inhibited (Pfizer,⁵ 1975; Monaghan, 1993); however, other researchers that have worked with elasmobranchs have shown OTC to have little adverse effects on growth (Tanaka [1990] for the Japanese Wobbegong [*Orectolobus japonicus*] and Gelsleichter et al. [1998] for the Nurse Shark [*Ginglymostoma cirratum*]). Further, this problem does not appear relevant in this study because fast (i.e., not inhibited) growth was observed with our OTC-marked juveniles.

Conclusions

Direct and indirect methods used in this study indicate rapid growth of juvenile Shortfin Mako in southern California and the OTC-marked vertebrae support a pattern of biannual deposition for the first 5 years of life. Accurate age and growth parameters in stock assessment models are important for fisheries management and are necessary for calculations of growth and mortality rates, age at recruitment, and longevity. This article highlights the need to continue life history studies of elasmobranch species throughout different regions and ocean basins.

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⁵ Pfizer, Inc. 1975. Oxytetracycline intramuscular solution leaflet 60-1051-00-8, 2 p. Pfizer Lab. Div., New York.

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Abstract—The modern fishery for Tilefish (*Lopholatilus chamaeleonticeps*) developed during the 1970s, offshore of southern New England, in the western North Atlantic Ocean. The population quickly became overexploited, with documented declines in catch rates and changes in demographic traits. In an earlier study, median size at maturity (L_{50}) of males declined from 62.6 to 38.6 cm fork length (FL) and median age at maturity (A_{50}) of males declined from 7.1 to 4.6 years between 1978 and 1982. As part of a cooperative research effort to improve the data-limited Tilefish assessment, we updated maturity parameter estimates through the use of an otolith aging method and macroscopic and microscopic evaluations of gonads. The vital rates for this species have continued to change, particularly for males. By 2008, male L_{50} and A_{50} had largely rebounded, to 54.1 cm FL and 5.9 years. Changes in female reproductive schedules were less variable among years, but the smallest L_{50} and youngest A_{50} were recorded in 2008. Tilefish are dimorphic, where the largest fish are male, and male spawning success is postulated to be socially mediated. These traits may explain the initial rapid decline and the subsequent rebound in male L_{50} and A_{50} and less dramatic effects on females. Other factors that likely contribute to the dynamics of maturity parameter estimates are the relatively short period of overfishing and the amount of time since efforts to rebuild this fishery began, as measured in numbers of generations. This study also confirms the gonochoristic sexual pattern of the northern stock, and it reveals evidence of age truncation and relatively high proportions of immature Tilefish in the recent catch.

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Changes in size and age at maturity of the northern stock of Tilefish (*Lopholatilus chamaeleonticeps*) after a period of overfishing

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As the largest malacanthid, growing to more than 1 m and 25 kg, the Tilefish (*Lopholatilus chamaeleonticeps*) is a valuable fishery species, often marketed as “golden tilefish.” The Tilefish ranges from New England to the Gulf of Mexico and into the Caribbean Sea (Freeman and Turner¹; Dooley, 1978), where 2 stocks have been identified, north or south of the Virginia and North Carolina border (Kitts et al., 2007). Northern Tilefish are morphologically and genetically distinct from southern Tilefish (Katz et al., 1983). Although individuals can range as far north as Nova Scotia, Tilefish are generally in low abundance in the Gulf of Maine (Able, 2002). Fishing on the northern stock is concentrated from Veatch Canyon, on the southern flank of Georges Bank off Massachusetts, to the Hudson Canyon off the coast of New Jersey (Grimes et al., 1980; Grimes and Turner, 1999; Kitts et al., 2007). Recent (2007–11) Tilefish landings north of the Caroli-

nas were valued at \$4.2–5.6 million annually.²

Unlike some historic fisheries of New England (e.g., Atlantic Cod [*Gadus morhua*], American Shad [*Alosa sapidissima*]; Lear, 1998), the Tilefish fishery developed only recently, and it had a most inauspicious start. The Tilefish was described in 1879 from fishery catches off New England (Goode and Bean, 1879). Occasional catches followed, but, in 1882, Tilefish became widely known because they constituted the largest single kill of vertebrates ever recorded. Tilefish are stenothermal, occurring along a narrow band of warm water, 9–14°C, at the continental shelf-slope break (Able et al., 1982; Grimes et al., 1986; Grimes and Turner, 1999); Marsh et al. (1999) assembled the evidence that this mass mortality was caused by intrusion of the Labrador Current into these outer shelf habitats. After a decade of no reported landings and speculation that this species had become extirpated in northern waters, landings resumed in the 1890s. Specific

¹ Freeman, B. L., and S. C. Turner. 1977. Biological and fisheries data on tilefish, *Lopholatilus chamaeleonticeps* Goode and Bean. NOAA Fisheries, Sandy Hook Lab. Tech. Ser. Rep. no. 5, 41 p. [Available from <http://www.nefsc.noaa.gov/publications/series/shltsr/shltsr5.pdf>, accessed October 2012.

² NOAA Fisheries, Annual Commercial Landings Statistics. http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html, accessed December 2012.

efforts to popularize Tilefish as a food fish resulted in record-high landings (4500 metric tons [t]) in 1916 (Freeman and Turner, 1977; Grimes and Turner, 1999). These efforts had only modest market success, and, except when prices were high, as in the 1920s and 1950s, landings rarely exceeded 1000 t until the 1970s (Fig. 1).

Events in the 1970s proved that persistent annual landings that exceeded 1000 t were unsustainable. Beginning in 1971, landings rose rapidly from <100 t to nearly 4000 t within a decade (Fig. 1). Landings remained high in the 1980s but were accompanied by evidence of overexploitation: decreased fish density, lower catch rates, smaller maximum size, and higher mortality (Grimes et al., 1980; Turner et al., 1983; Grimes et al., 1988; Grimes and Turner, 1999). By the 1990s, only a subset of the fleet remained dedicated to fishing for Tilefish in the northeastern United States, and a 2001 fishery management plan capped annual landings at 905 t (Kitts et al., 2007).

The northern Tilefish stock is now considered largely rebuilt but uncertainty in the stock assessment hampers confidence in stock status and projections (NEFSC³). There is, for example, no fishery-independent index of abundance, and monitoring of biological data has been infrequent. Comparisons of assessment model results indicate that the presence of large Tilefish, and the biomass estimate in general, is dependent on periodically strong year classes, such as the 1970 and 1973 year classes and most recently the 1993 and 1999 year classes (Turner, 1986; NEFSC³). High levels of exploitation during the 1970s and 1980s also may have altered the demographics of the population. Vidal (2010) reports a maximum age of Tilefish of 25 years, much younger than the maximum age of 46 years reported by Turner (1986), indicating that the population has not recovered from age truncation that occurred during the period of high exploitation.

This study updates several aspects of Tilefish life history from samples collected in cooperation with the commercial fishery. We began by revisiting the question of whether Tilefish are gonochoristic at the northern extent of their range (Dooley, 1978; Grimes et al., 1988). It has been proposed but not proven that Tilefish are functional hermaphrodites (Sadovy de Mitcheson and Liu, 2008); therefore, we examined and clarified the gonochoristic sexual pattern of the northern stock with gonad histology.

Ages were estimated with an otolith method, and age and size at maturity were calculated for both sexes to re-examine sexual dimorphism and temporal dynamics of

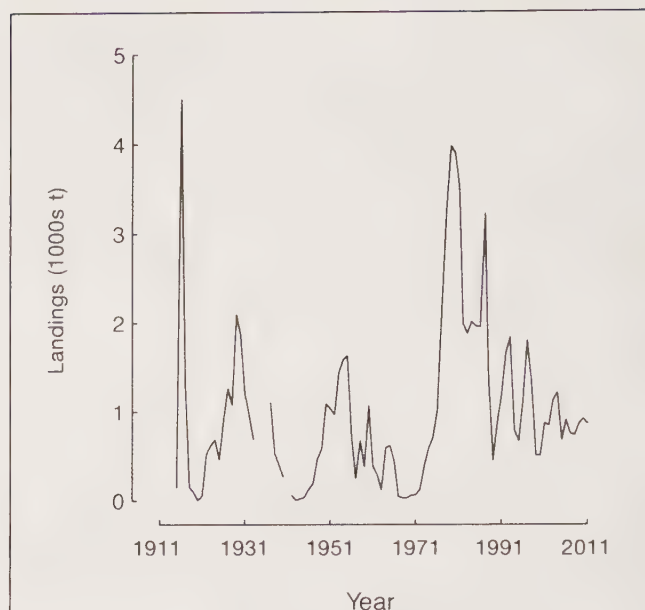


Figure 1

Tilefish (*Lopholatilus chamaeleonticeps*) landings from Virginia to New England for the period of 1915–2011 in thousands of metric tons (t). Landings from 1915 to 2008 are reported in NEFSC.³ Landing data for 2009–11 are from a NOAA Fisheries database (http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html, accessed December 2012).

maturity ogives. Male Tilefish grow faster and achieve a larger maximum size than females (Turner et al., 1983). Sexual dimorphism also is observed with respect to maturity: males develop larger predorsal adipose flaps than females at maturity, and males mature at older ages and larger sizes than do females (Grimes et al., 1988). Grimes et al. (1988) made 2 other important conclusions with respect to measurement of maturity: 1) males show evidence of spermiation, as detected by gonad histology, 1–2 years earlier than macroscopic ripening of the gonad, indicating that males delay spawning for a couple of years after this initial sign of maturity, and 2), from 1978 to 1982, male age at spawning declined about 2–3 years in association with high rates of exploitation and reduced population density. The effect was so extreme that, by 1982, males matured at a younger age than females (Fig. 2).

The topic of dramatic shifts in size and age at maturity was still controversial in the 1980s (Beacham, 1987), but such dynamic metrics have now been associated with overexploitation in Tilefish (Grimes et al., 1988) and other fish stocks (Trippel, 1995; Wright et al., 2011). To continue this line of inquiry, we compared our results with the benchmark values reported by Grimes et al. (1988). Although rapid responses by maturity traits to changes in mortality can be adaptive at the

³ NEFSC (Northeast Fisheries Science Center). 2009. Assessment of golden tilefish, *Lopholatilus chamaeleonticeps*, in the Middle Atlantic-Southern New England region. In 48th northeast regional stock assessment workshop (48th SAW) assessment report, p. 11–180. Northeast Fish. Sci. Cent. Ref. Doc. 09-15 [Available from <http://www.nefsc.noaa.gov/publications/crd/crd0915/pdfs/tilefish.pdf>, accessed February 2013.]

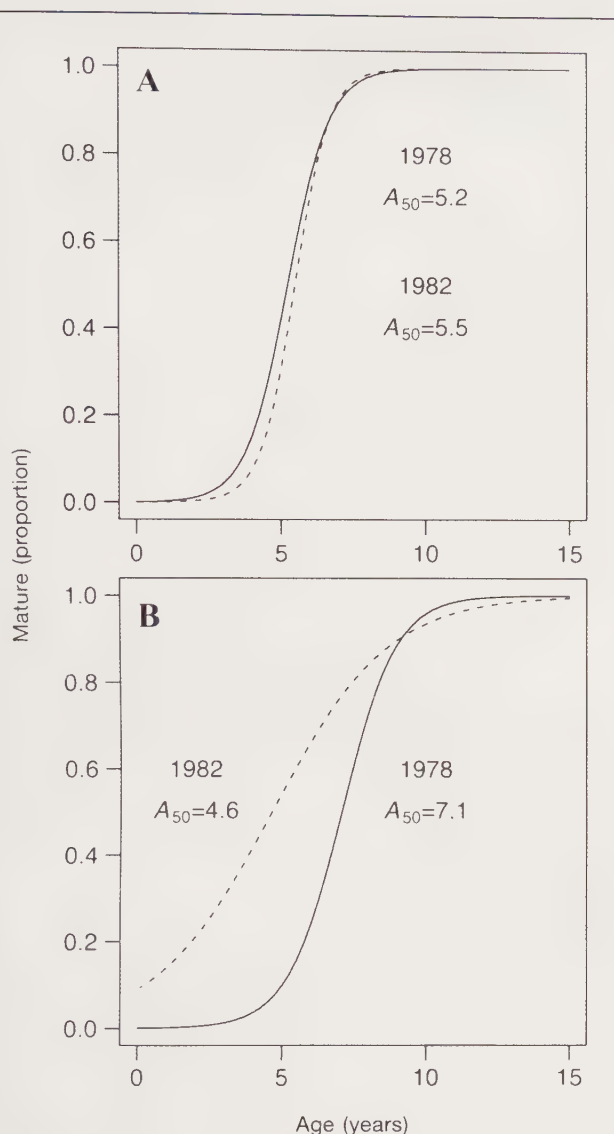


Figure 2

Maturity ogives for (A) female and (B) male Tilefish (*Lopholatilus chamaeleonticeps*) in 1978 (solid line) and 1982 (dashed line), at the height of the expansion of the modern fishery. Maturity was determined by macroscopic appearance of the gonad. Raw data were extracted from Grimes et al. (1988: tables 5 and 6). For model fitting, a generalized linear model and the logit link function in R software were used. The predicted curves together with the median age at maturity (A_{50}) are depicted by sex and year.

individual level, such responses can signal a decline in fishery yields and reproductive potential at the population level (Law, 2000; Fitzhugh et al., 2012; Cooper et al., 2013). Therefore, such data can be important to monitor and include in stock assessments (Caselle et al., 2011; Collins and McBride, 2011). In particular, the possibility that fishing selects for a certain genotype and

may thereby cause fishing-induced evolution can be a grave concern in terms of rebuilding fisheries to be sustainable (Conover, 2000; Heino and Dieckmann, 2008; Enberg et al., 2011).

Materials and methods

Field collections

During 2 trips by commercial fishing vessels targeting Tilefish in 2008, 688 Tilefish were sampled on 16 different days of normal longline operations. The first trip occurred in June, offshore of southern New England, where fish were collected between 70° and 72°W at depths of 104–280 m (Fig. 3). The second trip occurred in July, offshore of southern New England and farther south, where fish were collected between 70° and 74°W at depths of 119–283 m (Fig. 3). This geographic coverage overlapped all the major fishing areas by the Tilefish fishery north of the Carolinas (Turner et al., 1983; Kitts et al., 2007).

Fish were identified on the basis of taxonomic characters summarized by Able (2002). Fork length (FL) was measured to the nearest centimeter, and sex and maturity were determined macroscopically for 421 males and 267 females. Macroscopic determination of maturity followed Idelberger (1985; Table 1), which conforms to the standard maturity classifications used in the region (Burnett et al., 1989). To reduce cluster sampling in high-density areas, especially where fish from the same longline set may have had similar age or reproductive status, at least one fish of each sex was sampled for each 1-cm interval (Wigley et al., 1999; Helle and Pennington, 2004). This sampling strategy resulted in a broad range of fish sizes that was similar to the size composition in the landings, and, if anything, this strategy increased the number of larger, older fish to aid in fitting the maturity data to a model (Fig. 4).

Gonad histology

To confirm macroscopic evaluations of sex and maturity, gonad tissue was taken from 157 males and 67 females and fixed in 10% buffered formalin (Fig. 4B). Fixed tissue was prepared according to standard paraffin embedding techniques, stained with hematoxylin, and counterstained with eosin. Histological sections collected from 3 locations (anterior, medial and posterior) within the ovary lobe for 15 females were initially examined, but there was no effect of location on the most advanced stage of oocyte development, as also reported by Erickson et al. (1985); therefore, no further attention was given to the intragonad location.

The sexual pattern, meaning the functional expression of sexuality by individuals, was characterized on the basis of gonad histology. Morphological features noted were the presence of a remnant ovarian lumen

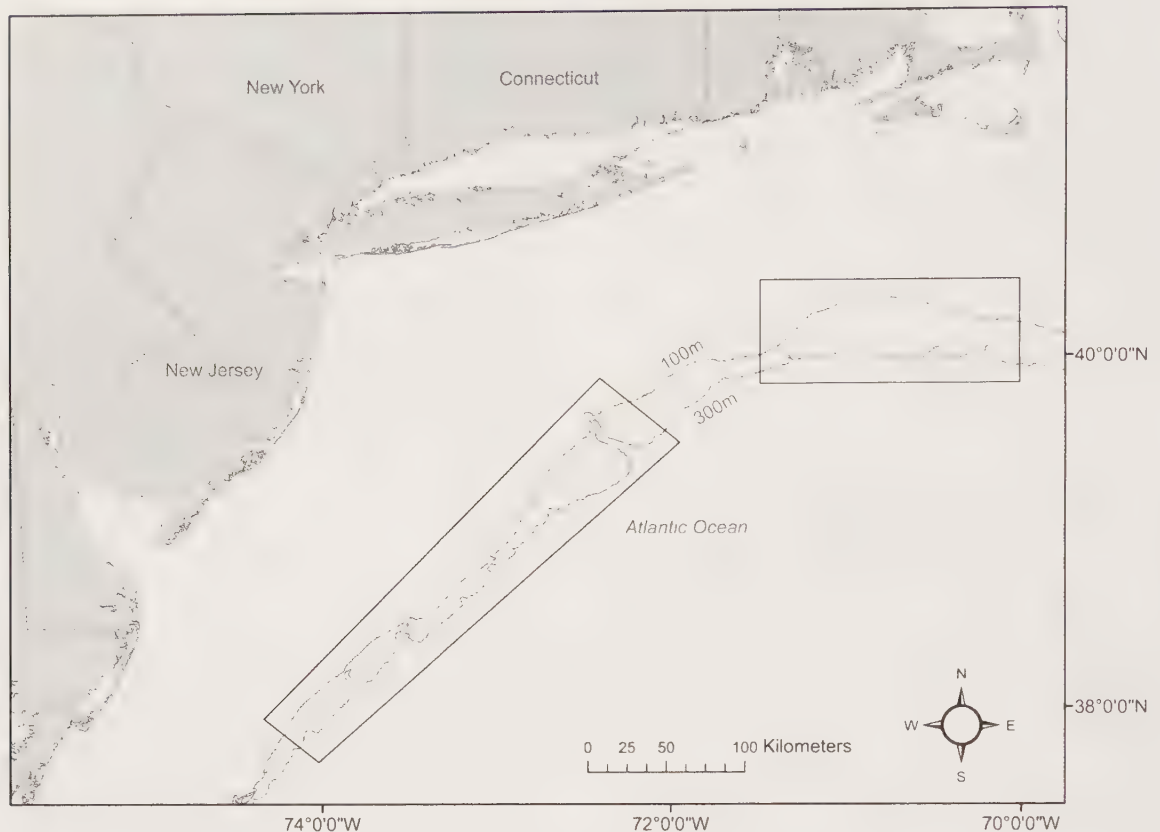


Figure 3

Map of areas where Tilefish (*Lopholatilus chamaeleonticeps*) were collected between the 100 and 300 m isobaths off southern New England in 2008 for this study to update the maturity schedules of this species. Fish were sampled during 2 trips by commercial fishing vessels targeting Tilefish: in June to the east (right polygon) and in July throughout the region (both polygons). The exact locations are not plotted to maintain confidentiality for commercial fishing operations.

in testes or a mix of ovarian and seminiferous tissue in a single gonad, the latter of which was reported by Grimes et al. (1988) and Erickson and Grossman (1986) for functional males. Although we examined morphology, our interpretation of sexual pattern was made on the basis of functionality, specifically whether gametogenesis was complete for both ovarian and seminiferous tissue during an individual's lifetime (Sadovy de Mitcheson and Liu, 2008). The existence of gonads that contained nonfunctional tissue of the opposite sex (i.e., intersex) and evidence that individuals matured and spawned as only one sex were considered to be a gonochoristic rather than a hermaphroditic trait. The infrequent presence of isolated oocytes in seminiferous tissue was not considered a bisexual condition because such oocytes also did not confer any function as a female (Sadovy and Domeier, 2005).

Because sampling occurred during the spawning season, the histological criterion for female maturity was the presence of secondary oocytes as the most advanced oocyte stage. Secondary oocytes were defined as germ cells that showed evidence of vitellogenin uptake

and transformation of lipoprotein yolk in the cytoplasm (Grier et al., 2009). Cortical alveolar-stage oocytes as the most advance stage were uncommon, and we comment on their presence and interpretation in the *Results* section. Male maturity was marked by the presence of spermatozoa in the spermatogenic lobules.

Age determination

Sagittal otoliths were extracted at sea and stored dry. These otoliths were thin-sectioned through the core according to standard methods with a low-speed, diamond-blade saw. Marginal increment analysis indicated that annuli are laid down by June of each year (Turner et al., 1983); therefore, given the timing of our collections, the number of complete bands equaled the age of the fish, in years.

Otoliths from 100 Tilefish used in Steve Turner's aging study (hereafter, called the *reference collection*) were used to train and calibrate the primary age reader (T. Vidal) in relation to the age-assignment practices reported in Turner et al. (1983) and Turner (1986).

Table 1

Macroscopic criteria for classifying maturity of Tilefish (*Lopholatilus chamaeleonticeps*), modified from Idelberger (1985: table 1), with references to new microscopic observations from gonad histology of Tilefish sampled in 2008 off southern New England for this study.

Maturity class	Description of ovary	Description of testes
Immature	Ovaries are small and transparent, becoming increasingly yellowish, rounded, and veined at the surface as fish nears maturity. Gonads compose <0.5% of body weight.	Testes consist of very narrow, transparent bands of tissue, composing <0.05% of body weight. Histological sections reveal isolated oocytes in a low percentage of young males.
Developing	Ovaries are firm, bulbous, yellow to light orange in color, and 0.5–2.0% of body weight. Vitellogenic (yolked) oocytes (0.3–0.7 mm in diameter) are visible through the gonad wall.	Gonads become opaque white, increasing modestly in size (0.03–0.12% of body weight).
Ripe	Enlarged gonads (1.0–5.0% of body weight) become lobular and have a speckled appearance. A homogenous mixture of vitellogenic and mature (hydrated; 0.7–1.0 mm) oocytes are evident through the gonad wall.	Further enlarged (0.1–0.2% of body weight) although still relatively small organs; long, flattened, and opaque milky white with phosphorescent sheen.
Running ripe	Ovaries are turgid and compose 5.0–10.0% of body weight. Gonads have a granular yellow appearance from vitellogenic oocytes in the lamellae and a transparent lumen containing hydrated oocytes, visible ventrally. Eggs (~1.2 mm) flow freely from the vent without any or only light pressure to the abdomen.	Sperm released with light abdominal pressure was diagnostic of this maturity class, although it also was observed rarely, even among the largest fish.
Spent	Gonads are reddish-orange, flaccid, and reduced to 0.5–1.0% of body weight.	Slightly flaccid and reduced to 0.04–0.07% of body weight.
Resting	Ovaries are uniformly yellow in color, becoming firm, composing 0.5–1.0% of body weight.	Indistinguishable from developing testes.

Training included testing for aging precision (i.e., repeatability of age assignment by different readers to the same otolith). Precision was first measured by percent agreement,

$$\text{Percent agreement} = 100 \times \frac{A}{N}, \quad (1)$$

where A = the number of replicate ages in agreement (of 2); and

N = the total number of fish aged.

Precision also was evaluated with Chang's coefficient of variation (CV; Chang, 1982):

$$CV = 100 \times \frac{1}{N} \sum_{j=1}^N \frac{\sqrt{\sum_{i=1}^2 \frac{(X_{ij} - X_j)^2}{R-1}}}{X_j}, \quad (2)$$

where N = the total number of fish aged;

X_{ij} = the i th age determination (i.e., of 2) of the j th fish; and

X_j = the mean age estimate of the j th fish.

Bowker's test was used to detect departures from symmetry between the new reader and the reference collection, with the formulation of Hoenig et al. (1995):

$$\chi^2 = \sum_{i=1}^{m-1} \sum_{j=i+1}^m \frac{(n_{ij} - n_{ji})^2}{n_{ij} + n_{ji}}, \quad (3)$$

where m = the maximum age in the data set; and

n_{ij} = the number of fish in the i th row and j th column, etc.

These precision tests also were used to evaluate repeatability of multiple readings by the primary age reader. In terms of final age assignment, when the first 2 readings from each otolith collected in 2008 disagreed, a third reading was performed. The value that occurred twice was used as the final age (i.e., there were no situations in which the third reading was different from both of the first 2 readings).

Models and analysis

Generalized linear models were programmed with R, vers. 2.15.2⁴ (R Core Team, 2012), to estimate parameters of maturity ogives. A full range of immature and mature fish, by size and age, was collected, making parameter estimation straightforward (Trippel and Har-

⁴ Mention of trade names of commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA

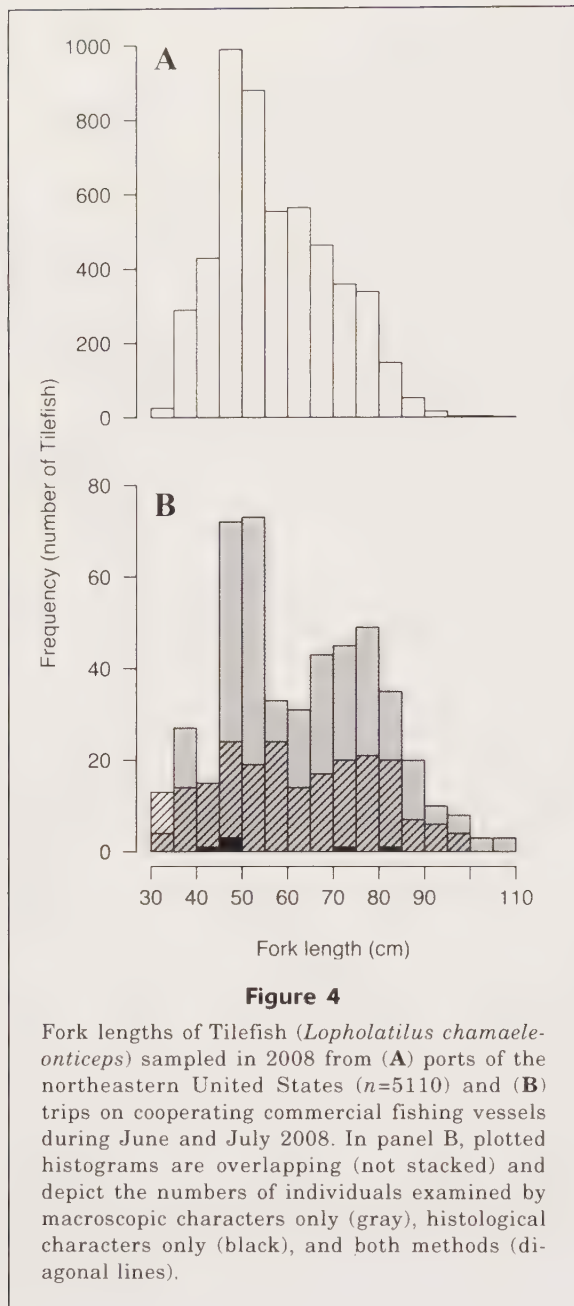


Figure 4

Fork lengths of Tilefish (*Lopholatilus chamaeleonticeps*) sampled in 2008 from (A) ports of the northeastern United States ($n=5110$) and (B) trips on cooperating commercial fishing vessels during June and July 2008. In panel B, plotted histograms are overlapping (not stacked) and depict the numbers of individuals examined by macroscopic characters only (gray), histological characters only (black), and both methods (diagonal lines).

vey, 1991). An information-theoretic approach was used to select among full and reduced models; the second-order Akaike's information criterion (AIC_c) was used to account for sample sizes in all comparisons.

Model selection began with evaluation of logit, probit, and complementary log-log model fits to FL or age, and histological maturity data, by sex. The logit model was selected because it consistently had a lower or a tied score ($<2 \Delta AIC_c$ value) compared with the score of the probit model and a much lower score than that of the complementary log-log model.

The logit-link function was used for selection of full or reduced models (i.e., by sex [logit {mature} ~ FL +

Sex + FL:Sex], method [macroscopic, histological], or year [1978, 1982, 2008]). Model results from 2008, as presented in Tables 2 and 3, are from analyses of individuals with both size and age data. Additional fish were measured for FL only, but inclusion of these fish in the analyses did not substantially change any results. Historic data were extracted from Grimes et al. (1988). Because FLs in Grimes et al. (1988: tables 3 and 4) were pooled by 5-cm bins, when entering their data for analysis, we assigned FL values for each fish as a midpoint value. Grimes et al. (1988: tables 5 and 6) reported older fish as a plus group (i.e., 15+); therefore, we also grouped all fish ≥ 15 years old together as a plus group to be consistent between studies, but the use of this plus group did not alter any result.

Results

Gonad histology

No seminiferous tissue was evident in any functioning females, but morphologically intersex males, occurring in 2 morphs, were observed (Fig. 5). In the first morph, a lumen was evident but seminiferous tissue arose directly along the gonad wall and no oocytes were present (Fig. 5A). Males with a lumen were common, but their frequency was not quantified because many histological sections were incomplete across the transverse plane and the lumen was relatively small and difficult to recognize in larger testes. The other morph of intersex males appeared as rare, isolated, primary growth oocytes interspersed in continuous seminiferous tissue (Fig. 5B). This morph was observed in 4 young fish, ages 3 or 5, and at least some of the embedded oocytes were visibly degrading. In other males, remnant gaps in seminiferous tissue were evident, indicating that isolated oocytes had been present but were now fully degraded (Fig. 5C).

The immature testis was initially dominated by spermatogonia surrounded by connective tissue, with limited spermatogenesis in the form of spermatocytes and spermatids in crypts surrounded by germinal epithelia (Fig. 5C). As spermatogenesis proceeded, spermatozoa were released into lobules lined with a discontinuous germinal epithelia (i.e., spermiation), signaling physiological maturity (Fig. 5D).

The ovary of immature females was dominated by oocytes at a perinucleolar stage (Fig. 5E). In many females classified as immature, the appearance of organelles (i.e., a Balbiani body) and early formation of cortical alveoli were common in the cytoplasm of the largest primary growth oocytes (Fig. 5F); we considered these traits characteristic of a maturing state (rather than a mature one), where such individuals were only preparing to mature and would not spawn until the following year. Only a single individual had advanced cortical alveoli as the most advanced oocyte stage (Fig. 5G), and 2 other females had only begun

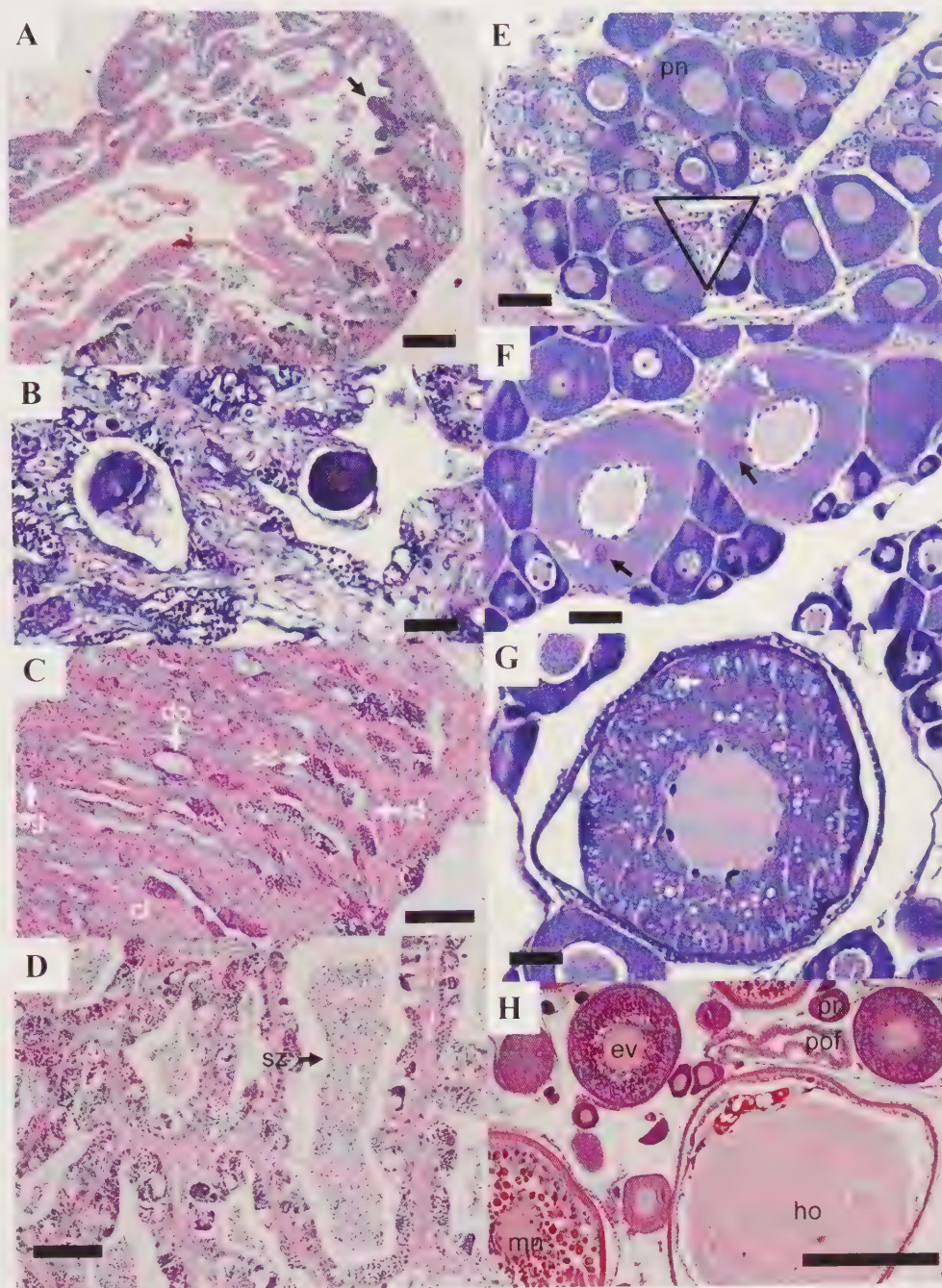


Figure 5

Microphotographs of gonadal tissue of Tilefish (*Lopholatilus chamaeleonticeps*) functional males (left) and females (right): (A) a functional male with seminiferous tissue developing directly along a lumen (arrow); (B) isolated oocytes, one partially degraded (left) and one intact (right), embedded in seminiferous tissue of a functional male; (C) seminiferous tissue of an immature male (ct=connective tissue, sg=spermatogonia, sc=spermatocytes, st=spermatids, do=degraded oocyte [fully degraded, no cell remaining]); (D) tissue of a mature (developing) male (sz=spermatozoa); (E) ovarian tissue of an immature female (pn=perinucleolar oocyte, triangle=oogonial nest); (F) primary growth oocytes, marking the Balbiani body (black arrow) and other inclusions that appear to be precursors to cortical alveoli (white arrow); (G) an oocyte with advanced cortical alveoli throughout the cytoplasm (arrow); and (H) ovarian tissue of a mature (ripe) female (ev=early vitellogenic oocyte [not fully with yolk], mn=migrating nucleus, ho=hydrated oocyte, pof=postovulatory follicle). Scale bars vary with image: 50 μ m (E, F, G, B), 100 μ m (C, D), 250 μ m (A), and 500 μ m (H).

vitellogenesis (not shown; i.e., the most advanced oocyte stage was only partially yolked, where the yolk inclusions did not extend from the nucleus to the chorion). These 3 fish were young, age 5 or 6, and, if they had been capable of spawning imminently, they evidently would have started spawning later than other conspecifics. In comparison, 92% of mature females were already actively spawning, with oocytes that either exhibited migrating nuclei or were in various stages of hydration; postovulatory follicles were observed as well (Fig. 5H).

Age determination

Tilefish otoliths are difficult to age, but good results were obtained after training the primary age reader

with the reference collection. There was 62% percent agreement with the reference collection (85% and 89% agreement within 1 or 2 years, respectively), with a Chang's CV of 5.1. There was a tendency to underage fish approximately 15 years old and older; however, Bowker's test indicated this departure was not significant ($\chi^2=19.5$; $P=0.42$).

Ages of Tilefish collected in 2008 ranged from 3 to 25 years for females and 3 to 23 years for males. Nearly all fish (98%; $n=180$) were ≤ 15 years old (Fig. 6). Precision, based on re-reading the 2008 otoliths, was good. Percent agreement between the first 2 readings was 79.6% (97% and 98% within 1 or 2 years, respectively), with Chang's CV of 2.2. Again, the Bowker's test of symmetry was not significant ($\chi^2=17.4$; $P=0.18$).

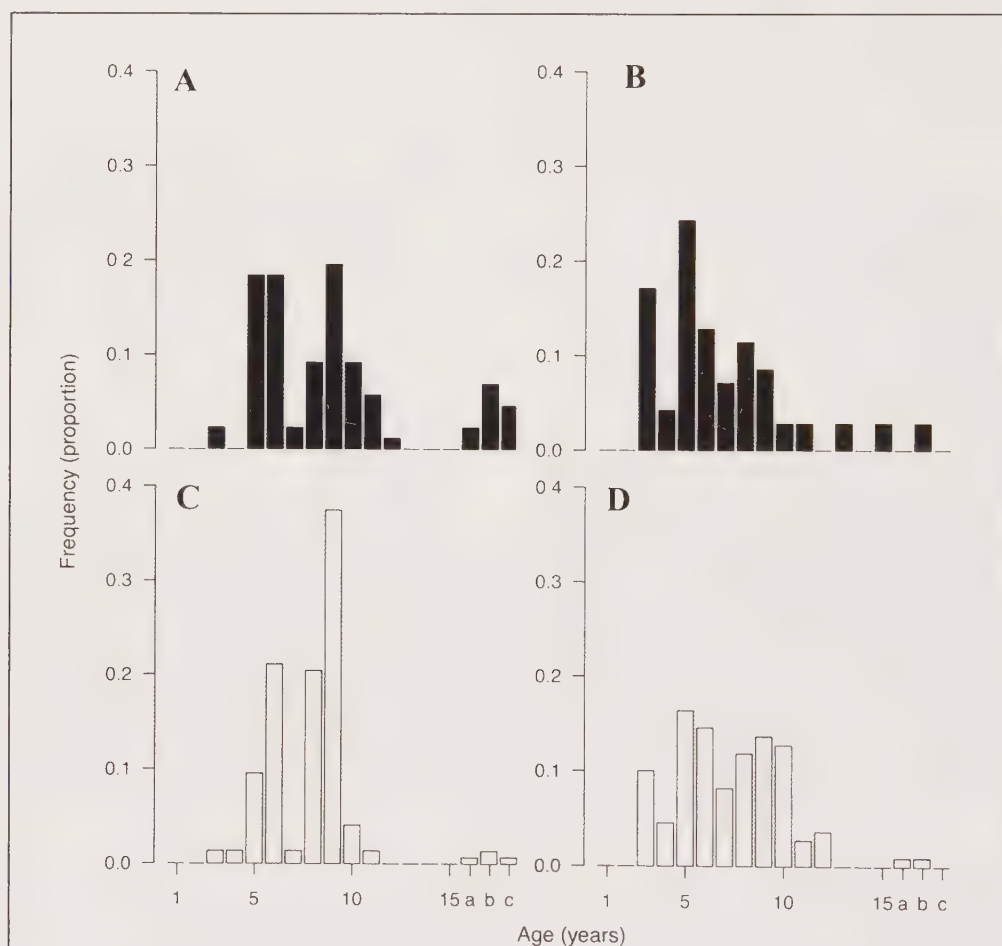


Figure 6

Ages of Tilefish (*Lopholatilus chamaeleonticeps*) collected by commercial longline vessels: (A) females in 1979 (number of fish [n]=87), (B) females in 2008 ($n=70$), (C) males in 1979 ($n=147$), and (D) males in 2008 ($n=110$). Assigned age is indicated along the x-axis; the oldest age classes are pooled (a: 16–20, b: 21–30, and c: >30 years old). Data for 1979 were transcribed from Turner (1986: appendices 1B, 1F), who reported grouped age classes >15 years.

Table 2

Median fork length (L_{50} , cm) and age (A_{50} , years) at maturity, standard error (SE), range, and sample size (n) of Tilefish (*Lopholatilus chamaeleonticeps*) collected in 2008 off southern New England—by year, sex, and method used to evaluate maturity. The methods used were macroscopic evaluation of the whole gonad and microscopic evaluation of gonad histology. Raw data from 1978 and 1982 are extracted from Grimes et al. (1988: tables 3–6; see text for details). Predicted ages at maturity from tabulated data in Grimes et al. (1988) also are plotted in Figure 2.

Year	Sex	Method	L_{50}	SE	Range	n	A_{50}	SE	Range ¹	n
2008	Male	Macroscopic	54.1	1.4	32–100	99	5.9	0.2	3–23	99
2008	Male	Histological	46.8	1.5	32–100	99	4.9	0.2	3–16	99
2008	Female	Macroscopic	44.1	1.1	32–90	58	4.9	0.2	3–25	58
2008	Female	Histological	46.3	1.2	32–90	58	5.2	0.2	3–21	58
1982	Male	Macroscopic	38.6	4.6	41–95	241	4.6	0.8	4–12	88
1978	Male	Macroscopic	62.6	1.0	31–115	384	7.1	0.2	4–15	246
1982	Female	Macroscopic	49.8	0.4	26–100	360	5.5	0.2	4–15	121
1978	Female	Macroscopic	45.4	1.2	31–95	393	5.2	0.1	4–15	267

¹Ages ≥ 15 years were grouped because Grimes et al. (1988) had grouped ages at this value in their data tables.

Maturity methods compared

Before we compared maturity schedules between years, we evaluated a potentially confounding effect on estimation of maturity of Tilefish: the effect of method. There was a general agreement in maturity classifi-

cation (i.e., immature versus mature) between macroscopic and microscopic (histological) methods. When both methods were used on the same fish, the agreement was higher for females (94%) than for males (84%). Mismatched females ($n=4$) were immature according to gonad histology but mature macroscopically.

Table 3

Comparisons of different data aggregates in testing for the effect of fish size (fork length [FL], cm) or age (years) on maturity of Tilefish (*Lopholatilus chamaeleonticeps*). The first comparison tests the effect of (A) method, macroscopic (macro) versus histological (histo), in evaluation of maturity status of fish collected in 2008 off southern New England for this study (controlling for factors of sex, M=male; F=female). The next comparison tests for (B) sexual dimorphism (by method with data from examination of fish collected in 2008). The last 2 comparisons test whether macroscopic estimates of maturity (used in all years) were different in 2008 than they were in (C) 1982 and (D) 1978, by using historic data for 1978 and 1982 from Grimes et al. (1988). See Table 2 for fitted parameter values by year, sex, and method. "Units" are modeled as a covariate, either as a main effect (+) or an interaction (*). Model sets are evaluated row-wise, with the second-order Akaike's information criterion (AIC_c) value. The lowest AIC_c value, indicating the least uncertainty, is underlined. If ΔAIC_c values are ≤ 2 , indicating the effects are indistinguishable, both or all cells are underlined.

AIC _c values of full and reduced models							
Units compared (covariates)	Other factors	Length models			Age models		
		FL* units	FL+ units	FL	Age* units	Age+ units	Age
A							
Method (macro/histo)	M, 2008	86.8	85.0	97.1	94.9	93.4	104.2
Method (macro/histo)	F, 2008	<u>55.8</u>	<u>53.9</u>	<u>53.8</u>	68.5	<u>66.5</u>	<u>66.0</u>
B							
Sex (male/female)	Macro, 2008	<u>74.7</u>	<u>74.9</u>	95.8	<u>87.3</u>	<u>85.9</u>	93.7
Sex (male/female)	Histo, 2008	<u>67.9</u>	<u>66.1</u>	<u>64.2</u>	<u>76.1</u>	<u>74.1</u>	<u>73.8</u>
C							
Year (1982/2008)	M, Macro	<u>305.3</u>	323.9	329.4	<u>143.4</u>	153.1	151.8
Year (1982/2008)	F, Macro	<u>189.8</u>	<u>187.8</u>	208.4	<u>78.7</u>	<u>77.2</u>	<u>78.8</u>
D							
Year (1978/2008)	M, Macro	<u>353.5</u>	356.6	369.7	<u>248.9</u>	<u>249.6</u>	261.5
Year (1978/2008)	F, Macro	<u>344.8</u>	353.8	352.8	<u>230.0</u>	<u>229.8</u>	<u>229.7</u>

Mismatched males ($n=25$) were mature according to histology but immature macroscopically.

Disagreements were for fish within the size range of transition from immature to mature (females: 42–49 cm FL; males: 44–71 cm FL). Mismatches among female classifications resulted in values of median size and age at maturity (L_{50} and A_{50} , respectively) that were 2.2 cm FL larger and 0.3 years older for histology-based results than for macroscopic classifications (macroscopic: $L_{50}=44.1$ cm FL, $A_{50}=4.9$ years; histological: $L_{50}=46.3$ cm FL, $A_{50}=5.2$ years) (Table 2). Mismatches among male classifications resulted in the L_{50} and A_{50} values that were 7.3 cm FL smaller and 1.0 year younger for histological examination than for macroscopic results (macroscopic: $L_{50}=54.1$ cm FL, $A_{50}=5.9$ years; histological: $L_{50}=46.8$ cm FL, $A_{50}=4.9$ years) (Table 2). Therefore, a histological method not only shifted the median parameter estimates in opposite directions for each sex, but the magnitude of uncertainty due to method was much greater for males than for females (Table 3A).

Maturity and spawning

The fishery harvests immature fish of both sexes. Macroscopic collections indicated that 14% of females (32–49 cm FL, 3–6 years old) and 38% of males (32–71 cm FL, 3–9 years old) caught on the 2008 sampled trips were immature.

Histological classifications did not support differences in L_{50} or A_{50} between sexes; however, macroscopic observations supported sexual dimorphism in the L_{50} and A_{50} parameters (Tables 2, 3B). These results likely mean that gonad histology detects hormonal maturation, a physiological state that occurs at a similar size and age for each sex but that may not be an accurate predictor of spawning activity for males. If so, then spawning activity, which is more closely aligned to measuring spawning stock biomass, occurred when males were 10 cm FL larger and 1 year older than females, on average, in 2008 (Table 2; Fig. 7).

Discussion

This study confirms that the northern stock of Tilefish is functionally gonochoristic. Grimes et al. (1988) also concluded that this stock is gonochoristic, noting the presence of isolated oocytes in 2 of 50 testes. They did not report finding a lumen in testes, but they may have overlooked it, stating they were unsure about the sexuality of small fish with a lumen. We observed that the lumen was not always obvious in large fish, even when looking for it. The term “prematurational sex change”—where individuals express themselves as a female first but do not mature as a female before they switch to a male—does not seem to apply here. Instead, we believe that a testis containing a lumen is a common feature in Tilefish, as occurs for other fishes (e.g., Pomacentri-

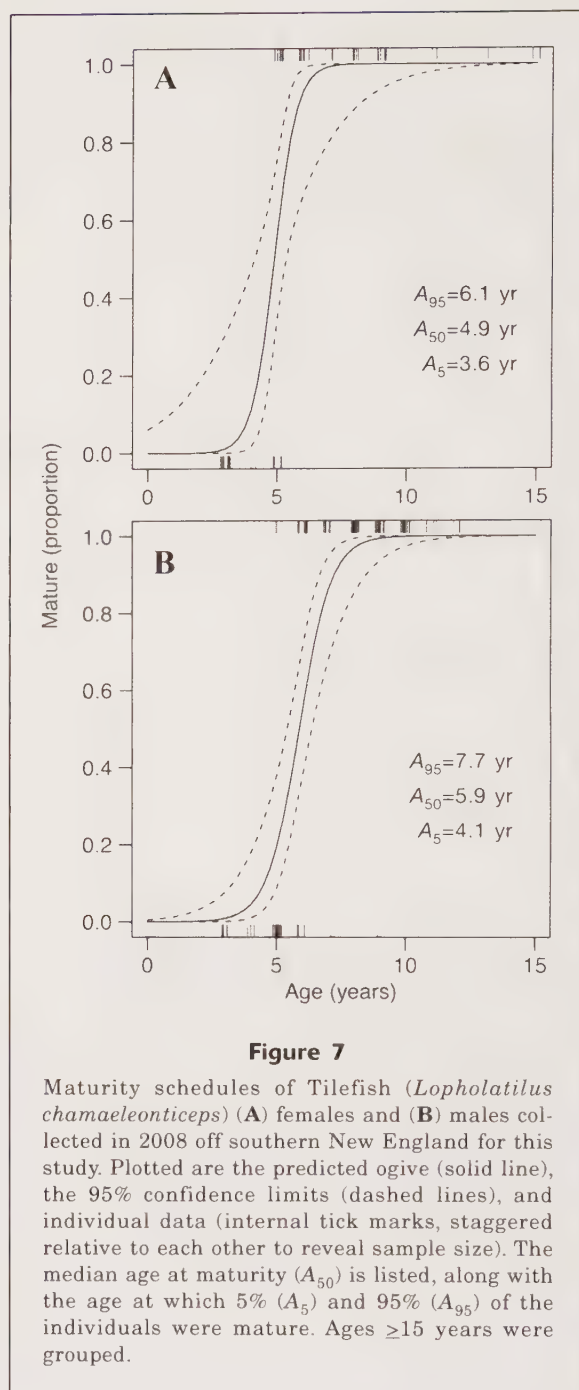


Figure 7

Maturity schedules of Tilefish (*Lopholatilus chamaeleonticeps*) (A) females and (B) males collected in 2008 off southern New England for this study. Plotted are the predicted ogive (solid line), the 95% confidence limits (dashed lines), and individual data (internal tick marks, staggered relative to each other to reveal sample size). The median age at maturity (A_{50}) is listed, along with the age at which 5% (A_5) and 95% (A_{95}) of the individuals were mature. Ages ≥ 15 years were grouped.

dae and Serranidae; Sadovy and Domeier, 2005), but is unrelated to function. We also do not categorize Tilefish as bisexual—a term that does not apply with the appearance of a lumen or the presence of isolated oocytes as described here (Sadovy and Domeier, 2005).

Our conclusion about gonochorism emphasizes function; in other words, all individuals reproduce exclusively as either male or female during their lives (Sadovy de Mitcheson and Liu, 2008). Because we sampled fish during the spawning period, and functional,

simultaneous hermaphroditism was not observed, this type of hermaphroditism is unlikely. We did not sample in winter to test for sequential sex change during the nonspawning period, but the histological evidence of similar A_{50} for both functional sexes makes this change unlikely. We predict that intersex fish would be no more common during the nonspawning season than they are reported herein for the spawning season. Also, we predict that, if collections of younger (<3 years old) fish were possible, isolated oocytes would be more commonly seen because isolated oocytes were observed to be degrading in our collections of testes. If these predictions about morphology are correct, they would confirm our conclusions that Tilefish are functionally gonochoristic. Erickson and Grossman (1986) investigated the sexual pattern of Tilefish farther south, in Atlantic waters of the Georgia Bight, and also concluded that Tilefish are functionally gonochoristic. In contrast, Lombardi-Carlson (2012) reported higher rates of intersex Tilefish in the Gulf of Mexico, evident for both functional males and females; therefore, there appears to be geographic variation in the morphological expression of intersex fish and possibly the sexual pattern by Tilefish.

Our study is the first attempt to age the northern stock of Tilefish in nearly 30 years. Turner et al. (1983) reported ages of fish collected in the longline and recreational fisheries in 1978, and Turner (1986) reported ages from the longline fisheries in 1979, 1980, and 1982. Females older than 31 years were collected in each of these sampling years, and males older than 31 years were collected in half of these years (Turner, 1986: appendix 1, A–H). The oldest fish observed was 46 years old (Turner, 1986), nearly twice as old as the oldest fish observed in 2008 in our study. Age structure during 1978–82 also appeared to be dominated by the 1970 and 1973 year classes, but dominant year classes (the most recent one being 1999; NEFSC³) were not obvious from the age structure measured in 2008 (Fig. 6). The reduced numbers of older fish today indicate that age truncation still exists, a finding that should not be surprising because landings >1000 t persisted well into the 1990s. We predict that fish older than 30 years will return to the population in the next decade.

The effect of method (macroscopic versus histological) in determination of maturity was more pronounced for males than for females (Tables 2, 3A). Differences in the 2008 female L_{50} and A_{50} attributable to method were minor (2.2 cm FL, 0.3 year). Our confidence in macroscopic evaluation of maturity was good at this time of year, when the main histological criterion, vitellogenic oocytes, were large enough (0.3–0.7 mm) to be seen macroscopically; hydrated oocytes were even more readily visible: 0.7–1.0 mm (as measured from histological slides by T. Vidal, unpubl. data). Data for females at other times of the year, especially during the nonspawning season, are likely to be less precise or accurate (Vitale et al., 2006; McBride et al., 2013).

That the observed differences in L_{50} and A_{50} attributed to method were larger for males (7.3 cm FL, 1.0 year) than for females was not unexpected. Grimes et al. (1988) also observed larger and older male L_{50} and A_{50} with a macroscopic method versus a histological method. We agree with Grimes et al. (1988): these differences in male maturity are not merely a methodological artifact but are of biological significance—likely the result of a physiological lag in gonad growth and the time that exists between spermiation (an indication of hormonal activity) and full ripening of the testes that precedes functional spawning by males. Such a lag may also be associated with behavioral differences. Grimes and Turner (1999) postulated that males first mature in a subordinate role and become dominate within 1–2 years.

Although such hypotheses demand further study, it is obvious that the method to determine maturity can matter in comparative analyses. The macroscopic method is likely aligned with functional spawning, and functional spawning more accurately defines spawning stock biomass. Therefore, it is the more appropriate method to use in routine measures to characterize this reference point for males. Grimes et al.'s (1988) approach emphasized the macroscopic method; therefore, our comparisons with relatively large sample sizes should be robust between all years (i.e., 1978, 1982, 2008).

The large percentage of immature Tilefish in the catch (14–38%, by sex) appears to point to violation of the principle to let fish reproduce at least once before they are harvested (Sissenwine and Shepherd, 1987). Although it is once again a topic of debate (Garcia et al., 2012), this principle prompts a re-evaluation of the effect of hook size on the proportion of immature fish landed.

Female size at maturity differed between 2008 and earlier years, but female age at maturity did not differ strongly between years (Tables 2, 3[C and D]). Female L_{50} was smaller in 2008 (44.1 cm FL) than in 1978 (45.4 cm FL) and 1982 (49.8 cm FL). The difference in A_{50} between all years was <1 year, and the low AIC_c score (i.e., <2) indicated that these differences in female A_{50} over time were similar. Nonetheless, female fitness is related to size and age (Green, 2008). In our study, the youngest A_{50} was measured in 2008. Other studies have shown that such shifts in maturity schedules are associated with reduced yield, survival, and fecundity (Law, 2000; de Roos et al., 2006; Conover et al., 2009). In particular, the mature female Tilefish that showed no immediate evidence of spawning were young (5–6 years old), indicating that newly matured females have lower spawning frequency and, therefore, a lower reproductive potential than older females. Age-specific effects on spawning frequency and batch fecundity are commonly observed in fishes and can alter stock assessment outcomes (Fitzhugh et al., 2012), and therefore continued research is warranted to clarify such

additional effects on reproductive potential of female Tilefish.

Male size and age at maturity differed between years much more dramatically than did female size and age at maturity (Tables 2, 3[C and D]). In 2008, male L_{50} was 54.1 cm FL, smaller than in 1978 (62.6 cm FL) but larger than in 1982 (38.6 cm FL). The same rebounding pattern was evident for male A_{50} , but, again, the difference in A_{50} between 1978 and 1982 (2.5 years) was not completely regained by 2008. Grimes et al. (1988) reported the initial trend, when they concluded that high fishing pressure was associated with and presumably induced a reduced size at maturity for males between 1978 and 1982. Our results indicate that this smaller size and younger age at maturity observed in 1982 did not become fixed. Because male fitness can be related strongly to size and age (Trippel, 2003), it is likely that male reproductive success is still hampered by reduced maturity parameters relative to that observed in 1978. The interpretation and predictability of these results, however, are hindered by the limited amount of data available to determine the stability of sex-specific maturity schedules between years.

Early reports that maturity schedules were flexible and could be dynamic in response to rates of fishing were treated with skepticism (Beacham, 1987), but they are becoming increasingly common and well supported (de Roos et al., 2006; Conover et al., 2009; Chuwen et al., 2011). If rates of maturation are heritable and survival rates of reproducing individuals are low, fishing will select individuals that reproduce at smaller sizes and younger ages (Reznick et al., 1990; Hutchings, 1993). If this selective pressure were to be eliminated, maturation rates would still likely require several generations to rebound (Conover et al., 2009). Tilefish have a minimum generation time of 5–7 years, according to the generation time estimated from the values of A_{50} reported here. Therefore, several generations actually have passed between 1982 and 2008. Also, the period of high exploitation (1977–87) did not extend beyond 2–3 Tilefish generations, unlike the several decades-long, chronic effects of overfishing observed in some other fisheries (Worm et al., 2009). Finally, Tilefish maturation evidently is not entirely under genetic control because males are presumed to use proximate sex and size cues to determine their reproductive potential (Grimes et al., 1988). In summary, we cannot rule out that genetic selection caused by increased fishing rates occurred 30 years ago for Tilefish, but we can point to these other factors as likely contributors to the appearance of a rebounding maturity rate among males following heavy exploitation in the 1970s and 1980s.

Conclusions

Intersex males exist, but the northern stock of Tilefish is functionally gonochoristic. Current demographics indicate age truncation and the lack of any strong year

classes in the rebuilt fishery of 2008. A macroscopic method for assessment of sex-specific maturity during the spawning season was verified as a reliable and cost-effective approach to monitoring trends in Tilefish maturation. Previously published data (Grimes et al., 1988) were reanalyzed, and an information-theoretic approach revealed differences in estimates of maturity ogives attributed to methods, sexes, and years.

Once method and sex were accounted for, it was evident that male maturation rates have rebounded from an earlier decline associated with a period of overexploitation. This rebound probably occurred because the period of overexploitation did not last long, several generations have passed during a period of improved conditions for the fishery, and male maturation is socially mediated. At present, only 3 years of age and maturity data exist, but these data were available for the 2009 Tilefish assessment, and they show the value of continued cooperative biological monitoring in this data-limited fishery.

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Abstract—The effects of El Niño–Southern Oscillation events on catches of Bigeye Tuna (*Thunnus obesus*) in the eastern Indian Ocean (EIO) off Java were evaluated through the use of remotely sensed environmental data (sea-surface-height anomaly [SSHA], sea-surface-temperature [SST], and chlorophyll-*a* concentration), and Bigeye Tuna catch data. Analyses were conducted for the period of 1997–2000, which included the 1997–98 El Niño and 1999–2000 La Niña events. The empirical orthogonal function (EOF) was applied to examine oceanographic parameters quantitatively. The relationship of those parameters to variations in catch distribution of Bigeye Tuna was explored with a generalized additive model (GAM). The mean hook rate was 0.67 during El Niño and 0.44 during La Niña, and catches were high where SSHA ranged from –21 to 5 cm, SST ranged from 24°C to 27.5°C, and chlorophyll-*a* concentrations ranged from 0.04 to 0.16 mg m⁻³. The EOF analysis confirmed that the 1997–98 El Niño affected oceanographic conditions in the EIO off Java. The GAM results indicated that SST was better than the other environmental factors (SSHA and chlorophyll-*a* concentration) as an oceanographic predictor of Bigeye Tuna catches in the region. According to the GAM predictions, the highest probabilities (70–80%) for Bigeye Tuna catch in 1997–2000 occurred during oceanographic conditions during the 1997–98 El Niño event.

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Effects of El Niño–Southern Oscillation events on catches of Bigeye Tuna (*Thunnus obesus*) in the eastern Indian Ocean off Java

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The El Niño–Southern Oscillation (ENSO) is a large-scale pattern of climate fluctuation that strongly influences much of the globe. In the Pacific, the ENSO cycle causes warm phases (El Niño) and cool phases (La Niña) that have been shown to affect catches in tuna fisheries (Lehodey et al., 1997; Lehodey, 2001). The approximate onset of the 1997–98 El Niño event occurred during March–April 1997, and the mature phase in November–December 1997 (Enfield, 2001). The El Niño event ended in May 1998 and a cold La Niña was established in the eastern Pacific. The 1997–98 El Niño was the strongest on record and affected the climate in many parts of the world (McPhaden, 1999). Catches of tunas around the world are affected by ENSO events (Howell and Kobayashi, 2006; Lehodey et al., 2010). Therefore, for sustainable management of Bigeye Tuna (*Thunnus obesus*) resources in the eastern Indian Ocean (EIO) off Java, one of the main islands in In-

donesia, understanding the effects of ocean climate variability on catch distribution is essential.

The Bigeye Tuna is a productive tropical species that accounts for more than 10% of the total catch of market tuna species worldwide (Miyake et al., 2010). Bigeye Tuna is a commercially targeted species and represents one of the most valuable species of longline fisheries in the EIO off Java (ISSF¹). It is a highly migratory species that is distributed between 40°N and 40°S in all 3 major oceans, except in the southwestern sector of the Atlantic (Hanamoto, 1987). Bigeye Tuna generally favor water temperatures between 17°C and 22°C. They prefer to stay near, and usually below, the

¹ ISSF (International Seafood Sustainability Foundation). 2012. ISSF stock status ratings—2012: status of the world fisheries for tuna. ISSF Tech. Rep. 2012-04, 88 p. [Available from <http://issf-foundation.org/resources/downloads/?did=328>, accessed November 2012.]

thermocline and come to the surface periodically (Peperell, 2010). The main depth range of fishing for Bigeye Tuna in the Indian Ocean is 161–280 m (Mohri and Nishida, 1999), although they can inhabit the depth range of 0–100 m during the night (Howell et al., 2010).

Sea-surface-height can be used to infer oceanic features such as current dynamics, fronts, eddies, and convergences (Polovina and Howell, 2005), and sea-surface temperature (SST) has been used to investigate productive frontal zones (Zainnudin et al., 2004), both of which can be used to indicate potential tuna fishing grounds. Thermal (or color) gradients in satellite images that arise from the circulation of water masses often indicate areas of high productivity (Saitoh et al., 2009). Chlorophyll-*a* data can also be used as a valuable indicator of water mass boundaries and may identify upwelling that can influence tuna distribution in a region.

The effects of ENSO on oceanographic conditions and tuna catches in the Pacific have been reported widely (Lehodey et al., 1997; Torres-Orozco et al., 2006; Briand et al., 2011). High catch rates of Albacore (*Thunnus alalunga*) in the southwest Pacific Ocean were found to correspond with high negative Southern Oscillation Index values during strong El Niño events (Briand et al., 2011). The effects of ENSO events on Bigeye Tuna catches have been well studied in the western Pacific Ocean (Miller, 2007) but less studied in the Indian Ocean. Most Indian Ocean studies have focused on the relationship between oceanographic parameters and the distribution of Bigeye Tuna (Mohri and Nishida, 1999; Song et al., 2009; Song and Zhou, 2010), the correlation of a single oceanographic factor with ENSO (Yoder and Kennely, 2003), or oceanographic variability in the interior Indonesian seas (Zhou et al., 2008; Sprintall et al., 2009).

Here, we focus on the ways in which climate variability affects oceanographic conditions and catch rates of Bigeye Tuna in the EIO off Java. To obtain a more detailed description of the spatiotemporal characteristics of those oceanographic parameters, we applied the empirical orthogonal function (EOF). Further analysis was undertaken with a generalized additive model (GAM) to examine the relationship between oceanographic conditions and catch rates of Bigeye Tuna. The ultimate goal of this study was to understand how catch rates of Bigeye Tuna in the EIO off Java are affected by ENSO events.

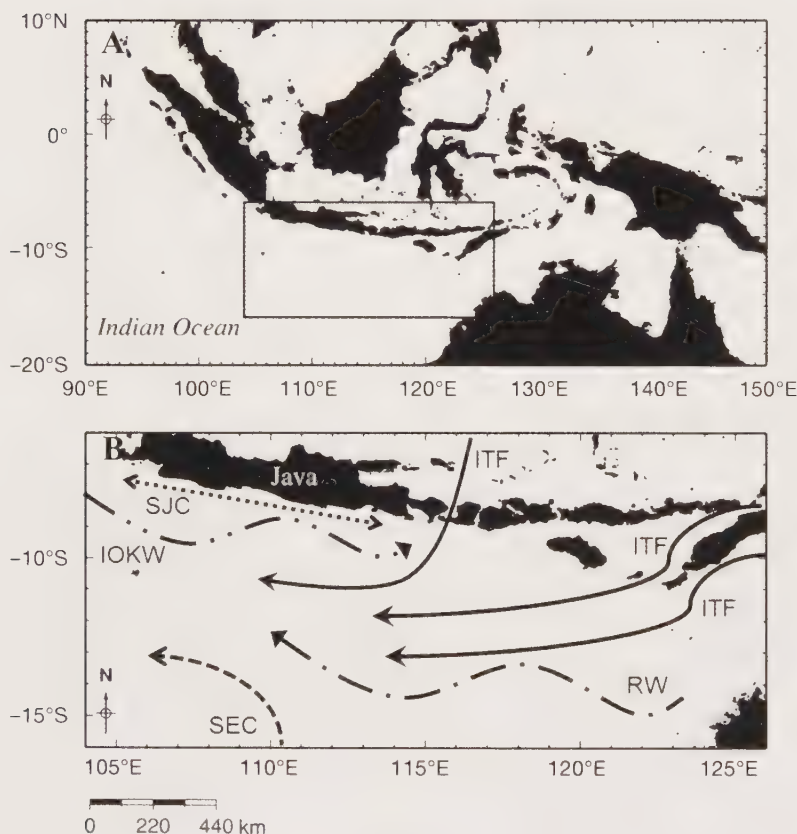


Figure 1

(A) Map of the Indonesian seas, with the inset box representing the study area. (B) Map of the study area in the eastern Indian Ocean (EIO) off Java for our analyses of how El Niño–Southern Oscillation events may affect catch rates of Bigeye Tuna (*Thunnus obesus*). In panel B, the wave and current systems in the EIO off Java are indicated by the dotted line for the South Java Current (SJC), solid lines for the Indonesian Throughflow (ITF), the line with dashes and 2 dots for the Indian Ocean Kelvin Waves (IOKW), the line with dashes and 1 dot for the Rossby Waves (RW), and the dashed line for the Indian Ocean South Equatorial Current (SEC).

Materials and methods

Study area

The study area was located in the EIO, south of Java, spanning between 6–16°S and 104–126°E (Fig. 1B). This area has complex dynamic currents and wave systems. The dominant current and wave features include 1) the Indonesian Throughflow (ITF), outflow water from the Pacific to the Indian Ocean (Molcard et al., 2001; Gordon et al., 2010); 2) the seasonally reversing South Java Current (SJC) along the southern coast of the Indonesian Sea (Sprintall et al., 2010); 3) the Indian Ocean South Equatorial Current (SEC) that flows from the southern Indian Ocean to an area off southern Java (Zhou et al., 2008); 4) downwelling Indian Ocean Kelvin Waves (IOKW) that propagate to the east along the coasts of west Sumatra, Java, and the lesser Sunda islands (Syamsudin et al.,

2004); and 5) westward Rossby Waves propagation at 12–15°S (Gordon, 2005; Sprintall et al., 2009).

Besides these current and wave systems, winds over the Indonesian maritime continent and the position of the Intertropical Convergence Zone are dominant features of strong monsoon signatures. During the south-east monsoon (May to October), southeasterly winds from Australia generate upwelling along the southern coasts of Java and Bali. These conditions are reversed during the northwest monsoon (November to April) (Gordon, 2005).

Data

For our study, we used fishery catch data and satellite remotely sensed data. Bigeye Tuna catch data and remotely sensed environmental data for the period of 1997–2000 were analyzed. These data included the ENSO components of an El Niño event (April 1997–May 1998) and a La Niña event (July 1998–June 2000).

Fisheries data sets Catch data for Bigeye Tuna were obtained from longline fishing logbooks provided by PT Perikanan Nusantara,² an incorporated company of the Indonesian government, at Benoa, Bali. Data included fishing position (latitude and longitude), operational days, fish weight (in kilograms), vessel number, number of hooks, and the number of fish caught per month during 1997–2000. The fishing locations recorded in the logbook were only the fishing positions where Bigeye Tuna were caught (there were no data for the locations where no fish were caught). These data were compiled into grids of 1° latitude × 1° longitude because catch data for Bigeye Tuna were available only at a resolution of 1°. From this data set, the catch rate of Bigeye Tuna was expressed as a percentage of hook rate (HR). The HR was calculated as the number of fish caught (individuals/month) per 100 hooks. The HR, therefore, shows how many tuna were hooked per unit of 100 longline hooks, and the HR can be referred to as catch per unit of effort.

The majority of fishing operations were conducted by medium-size vessels (100 gross tonnage). The number of vessels in operation was 19–20 per month, and vessels used the same fishing gear (longline sets) and similar fishing techniques. The number of fishing sets was within the range of 910–1607 per year. The longline sets were specifically designed and constructed to reach the swimming depths of the Bigeye Tuna. PT Perikanan Nusantara³ used 2 types of longline sets constrained by the fishing depth during operation: 1) a shallow set (depth <100 m; consisting of 4–6 branch lines between floats) and 2) a deep set (depth 100–300

m; consisting of 10–14 branch lines between floats). The deep set was used to catch Bigeye Tuna, and the shallow set was better suited to catch Yellowfin Tuna (*Thunnus albacares*). The longline fishery targeted Bigeye Tuna at operational depths of 109–288 m during night sets. Each deep set consisted of 10–14 branch lines between floats and 800–1600 hooks per set. The fishing ground covered an area located around 10–16°S and 108–120°E; fishing operations were limited to 15 days per trip because of fuel costs and the need to keep caught fish fresh (Perikanan Nusantara³).

Bigeye and Yellowfin Tunas were distinguished by various characteristics, including the following features: the Bigeye Tuna is longer, has a large head, large eyes, a dusky-colored tail, yellowish finlets edged in black, and a tail with a flat, trailing edge. The Yellowfin Tuna is shorter, has a smaller head, round and small eyes, a narrow body, a yellowish tail, and a notch in the center of its tail (Itano⁴).

Remotely sensed data Remotely derived environmental variables included the sea-surface-height anomaly (SSHA), SST, and chlorophyll-*a* concentration. The SSHA data with a spatial resolution of 1/3°, derived from the TOPEX/Poseidon and ERS-1/2 altimeter measurements, were produced and distributed by Archiving, Validation and Interpretation of Satellite Oceanographic Data (AVISO, <http://www.aviso.oceanobs.com>). We obtained 7-day composite cycles of SSHA products to calculate the monthly mean SSHA. SST data were derived from the Advanced Very High Resolution Radiometer sensor on board NOAA satellites. This data set is distributed by the Physical Oceanography Distributed Active Archive Center (<http://podaac.jpl.nasa.gov>) of the Jet Propulsion Laboratory of the National Aeronautics and Space Administration (NASA). We used the monthly mean SST data set at a pixel resolution of 4 × 4 km. Chlorophyll-*a* data were derived from images obtained from the

Sea-viewing Wide Field-of-view Sensor (SeaWiFS) Project (level 3) and were of a spatial resolution of 9 × 9 km for the period from September 1997 to December 2000 (monthly composite data were downloaded from <http://oceancolor.gsfc.nasa.gov>). These data were processed with the SeaWiFS Data Analysis System virtual appliance (SeaDAS VA, vers. 6.1) of NASA (<http://seadas.gsfc.nasa.gov/seadasva.html>).

SSHA and SST images were matched with the 9-km-resolution spatial scale for chlorophyll-*a* concentrations. The 9-km-resolution data were used to capture dynamic features of the oceanographic conditions that represented El Niño and La Niña events and to show spatial patterns for the EOF analysis. However, for the

² Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

³ Perikanan Nusantara, Inc. 2001. Vessels operation data of Incorporated Company of Perikanan Nusantara, 78 p. Perikanan Nusantara, Jakarta, Indonesia.

⁴ Itano, D. G. 2005. A handbook for identification of yellowfin tuna and bigeye tuna in fresh condition, vers. 2, 27 p. Pelagic Fisheries Research Program, Univ. Hawaii, Honolulu. [Available from ftp://ftp.soest.hawaii.edu/PFRP/itano/1_BE-YF%20ID%20Fresh_ENGLISH_v2_logo.pdf, accessed November 2012.]

GAM input, SSHA, SST, and chlorophyll-*a* data were calculated on a spatial grid of $1^\circ \times 1^\circ$ to match with the spatial resolution of the fisheries data. We resampled the remotely sensed data to resolutions of 9 km and 1° through the use of geographic information system tools, including Generic Mapping Tools (GMT, vers. 4.5.7 [Wessel and Smith, 1998]), with the nearest-neighbor technique. Nearest-neighbor assignment can be applied with the resample function as a preprocessing step before combination of raster data of different resolutions. This assignment does not change any of the values of cells from the input raster data sets; the cell center from the input raster that is closest to the cell center for the output processing is used.

Niño 3.4 index The Niño 3.4 index was used as a climatic index of ENSO indicators based on SST. The index is the average SST anomaly in the region bounded by 5°N to 5°S and 120°W – 170°W . The Niño 3.4 index was downloaded from the NOAA Climate Prediction Center (<http://www.cpc.ncep.noaa.gov>). El Niño and La Niña events were identified if the 5-month running average of the Niño 3.4 index exceeded $+0.5^\circ\text{C}$ for El Niño or -0.5°C for La Niña for at least 5 consecutive months (this index is shown as the dashed line in Fig. 2A).

Catchability coefficient

Catchability was defined as the proportion of available fish in the population that would be caught by a unit of fishing effort. Catchability depends on the distribution of fishing effort in relation to the distribution of the target species (Ellis and Wang, 2007). The catchability coefficient is defined as the proportion of the total stock taken by one unit of effort (Haddon, 2011) and is expressed as

$$C / (q E) = B, \quad (1)$$

where C = catch;
 q = the catchability coefficient;
 E = the amount of fishing effort; and
 B = stock biomass.

The unit of effort used for calculation of longline catch rates is the number of hooks, as a result of changes in gear practices (Ward and Meyers, 2004). We computed the catchability coefficient for all months during 1997–2000.

Empirical orthogonal function

We applied the EOF as a statistical method to quantitatively examine oceanographic parameters. EOF analysis is a useful technique for decomposition of a time series of geophysical data into temporal and spatial variability in terms of orthogonal functions or statistical modes. EOF analysis has been used commonly to describe spatiotemporal ocean variability (Yoder and

Kennely, 2003; Otero and Siegel, 2004; Radiarta and Saitoh, 2008; Tolan and Fisher, 2009).

EOF analysis was applied to the raw weekly data set of SSHA and SST and monthly data of chlorophyll-*a* concentrations because of a lack of data in many of the weekly images. Here, we examined only the first and second dominant modes, which were statistically independent and significant. A more comprehensive explanation of the concept of EOF analysis has been provided by Bjornsson and Venegas (1997). We constructed the EOF analysis using Matlab, vers. 7.1, software (The MathWorks, Inc., Natick, MA). On the basis of the results of the EOF, we generated maps of patterns of spatial and temporal ocean variability in the EIO off Java with ArcGIS tools (Esri, Redlands, CA).

Generalized additive model

The GAM was first proposed by Hastie and Tibshirani (1990). The advantage of this model is that the predictor variables have nonlinear effects upon the response variable. We applied the binomial GAM to analyze positive catches, interpreted as presence (1), and null catches, interpreted as absence (0) (Fraile et al., 2010), of Bigeye Tuna and to determine the catch probability of Bigeye Tuna in the EIO off Java. The Bigeye Tuna catch data presented here are based only on the grids fished because, as mentioned previously, catch information for Bigeye Tuna was not available for unfished grids; therefore, we ignored the unfished strata (Walters, 2003). Some sampling bias may have affected our results regarding catch variability. However, the catch data are nevertheless useful for examination of Bigeye Tuna variability in the study area, and the HR data based on those catch data may be indicative of relative changes in availability. We analyzed the presence of Bigeye Tuna through exploration of the spatial trends in their catch distribution that were influenced by SSHA, SST, and chlorophyll-*a* concentrations. All explanatory model terms were treated as continuous variables and the spline smoothers were fitted initially to each term in the model (Zuur et al., 2009). A stepwise GAM was performed to determine the best-fitting model before application of the final GAM to the entire data set. Akaike's information criteria (AIC) were used to determine the optimal set of explanatory variables. The model with the smallest AIC can be selected as the optimal model. GAMs were constructed in R software (vers. 2.14.0; R Development Core Team, 2011) with the gam function of the mgcv package (Wood, 2006). The GAMs were fitted in the form

$$g(u_i) = \alpha_0 + s_1(x_{1i}) + s_2(x_{2i}) + s_3(x_{3i}) + s_n(x_{ni}), \quad (2)$$

where g = the link function;
 u_i = the expected value of the dependent variable (Bigeye Tuna catch);
 α_0 = the model constant; and

s_n = a smoothing function for each of the model covariates x_n .

The constructed GAM could then be used to predict the Bigeye Tuna catch probability with the predict.gam function in the mgcv package in R (Wood, 2006). The Bigeye Tuna catch probability is the relative probability of catching one or more Bigeye Tuna at a location given the oceanographic conditions in the area (Teo and Block, 2010). The prediction maps were produced with the best model selected from a set of 7 models. The distribution of the GAM-predictions of Bigeye Tuna catch was compared with monthly fishery data. With GMT tools, we made monthly predictions of Bigeye Tuna catch probabilities.

Results

Catch rates of Bigeye Tuna

During the El Niño event in 1997–98, catch rates of Bigeye Tuna peaked in May–July 1997 (0.87–0.94 HR) and were still high in February–July 1998 (0.69–0.90 HR), followed by a continuous decline in the later months of 1998 (Fig. 2A). During the La Niña event in 1999–2000, catch rates were reduced throughout the year (HR < 0.67). The average HR was higher during the 1997–98 El Niño event (0.67) than during the 1999–2000 La Niña event (0.44).

The number of hooks deployed ranged from 14,392 to 178,109 per month (Fig. 2B), and more hooks were used during the 1997–98 El Niño event (147,676 hooks) than during the 1999–2000 La Niña event (144,283 hooks). In June 1997, 178,109 hooks (maximum number) were deployed and in November 2000, 14,392 hooks (minimum number) were deployed. The catchability coefficient (q) varied with the number of hooks (Fig. 2B). Catchability was high in May 1997 (1.56×10^{-7}), June 1998 (1.47×10^{-7}), and November 2000 (2.73×10^{-7}).

Catch rates of Bigeye Tuna showed seasonal variations and were higher during the southeast monsoon (May–October; SE) than during the north-

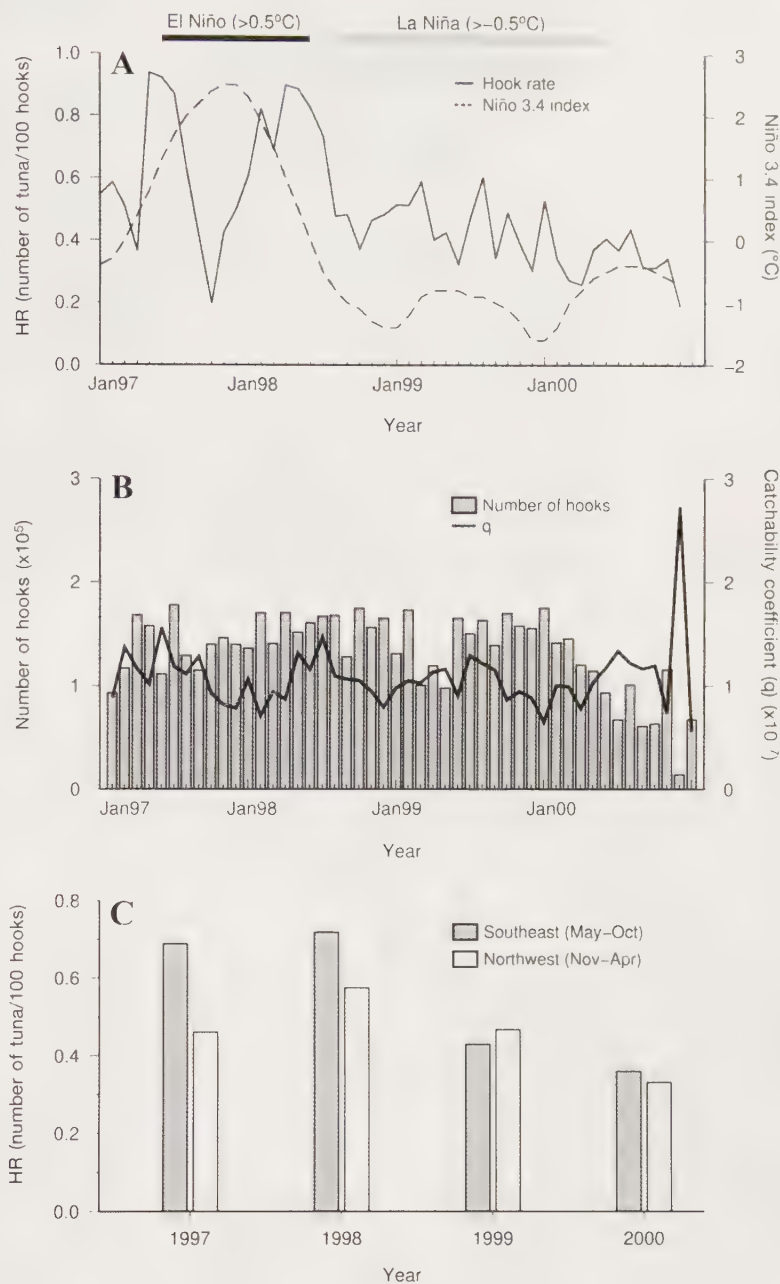


Figure 2

(A) Variability in catch rates of Bigeye Tuna (*Thunnus obesus*) in the eastern Indian Ocean off Java by hook rate (HR) percentage (solid line) and SST anomalies from the Niño 3.4 index during 1997–2000 (dashed line). El Niño and La Niña events were identified when the average of the Niño 3.4 index exceeded $+0.5^{\circ}\text{C}$ for El Niño or -0.5°C for La Niña for at least 5 consecutive months. The El Niño event is indicated by a black bar on the top of this graph, and the La Niña event is indicated by a gray bar on the top. (B) The total number of hooks deployed (gray bars) and time series variation of the catchability coefficient (solid line) during 1997–2000. (C) Seasonal variations in Bigeye Tuna HR in 1997–2000. The gray bar represents the southeast monsoon (May–October), and the white bar represents the northwest monsoon (November–April).

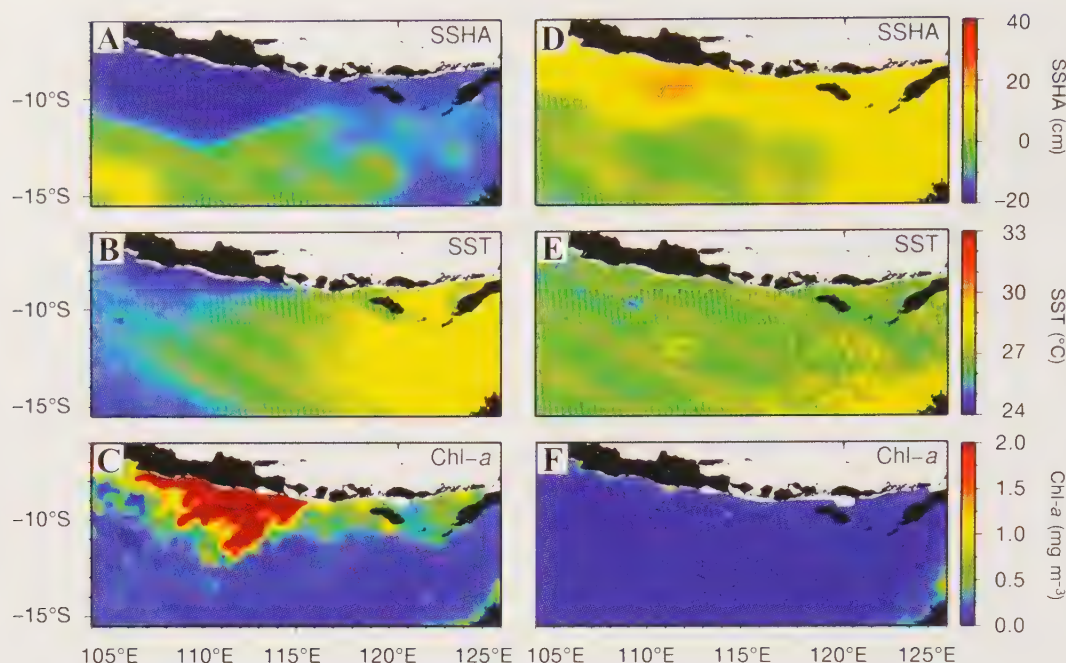


Figure 3

On the left, images of mean values for 3 months obtained from remotely sensed data of the eastern Indian Ocean off Java during El Niño event (September, October, and November 1997) for 3 parameters—(A) sea-surface-height anomaly (SSHA), (B) sea-surface temperature (SST), and (C) chlorophyll-*a* (chl-*a*) concentration. On the right, images of mean values for 3 months obtained during La Niña event (February, March, and April 1999) for the same 3 parameters: (D) SSHA, (E) SST, and (F) chl-*a* concentrations. Scale units are in centimeters, degrees Celcius, and milligrams per cubic meter for SSHA, SST, and chl-*a* data, respectively.

west monsoon (November–April; NW) for all years except 1999 (Fig. 2C). High HRs (average 0.55 HR) were recorded during the southeast monsoon, and lower HR (average 0.45 HR) occurred during the northwest monsoon.

Features of oceanographic conditions

The following results are presented to show how the different phases of ENSO affected oceanographic conditions in the EIO off Java. Figure 3 shows 6 snapshots of SSHA, SST, and chlorophyll-*a* conditions, each showing the means of values from 3 different months during different phases of El Niño (mean of September, October, and November 1997) and La Niña (mean of February, March, and April 1999) in the EIO off Java. The months that represent the El Niño and La Niña events were chosen on the basis of the 3 consecutive months with the highest individual values in the Niño 3.4 index during El Niño and La Niña during 1997–2000. There were contrasting conditions of SSHA and SST along the coasts and in offshore areas during the El Niño and La Niña events.

During the El Niño event, SSHA showed negative values (from -1 to -20 cm) along coastal regions of the

EIO off Java (Fig. 3A). In contrast, offshore regions influenced by frontal areas between 10 – 12°S and 15°S exhibited positive SSHA (4 cm). Lower SST (24 – 27°C) occurred in the coastal to offshore regions of the EIO off Java (Fig. 3B), and warmer waters (29°C) appeared in the eastern part of the EIO off Java. Conversely, during the La Niña event, positive SSHA (1 – 13 cm) occurred along the coasts, and negative SSHA (-5 to -3 cm) were found offshore between 12° and 16°S (Fig. 3D). SST during the La Niña event both near the coasts and in offshore areas of the EIO off Java (27 – 29°C) were higher than values during the El Niño event in this region (Fig. 3E).

Chlorophyll-*a* concentrations were higher during the El Niño event (0.2 – 2.0 mg m^{-3} ; mean of September, October, and November 1997; Fig. 3C) than they were during the La Niña event (0.05 – 0.10 mg m^{-3} ; mean of February, March, and April 1999; Fig. 3F). The highest concentration of 2 mg m^{-3} was detected during the El Niño event along the coast of the EIO off Java, and values decreased toward offshore (0.01 – 0.20 mg m^{-3}) around the frontal area at 10 – 12°S (Fig. 3C). This variation in chlorophyll-*a* values coincides well with the occurrence of lower SST in the same areas during the El Niño event (Fig. 3B).

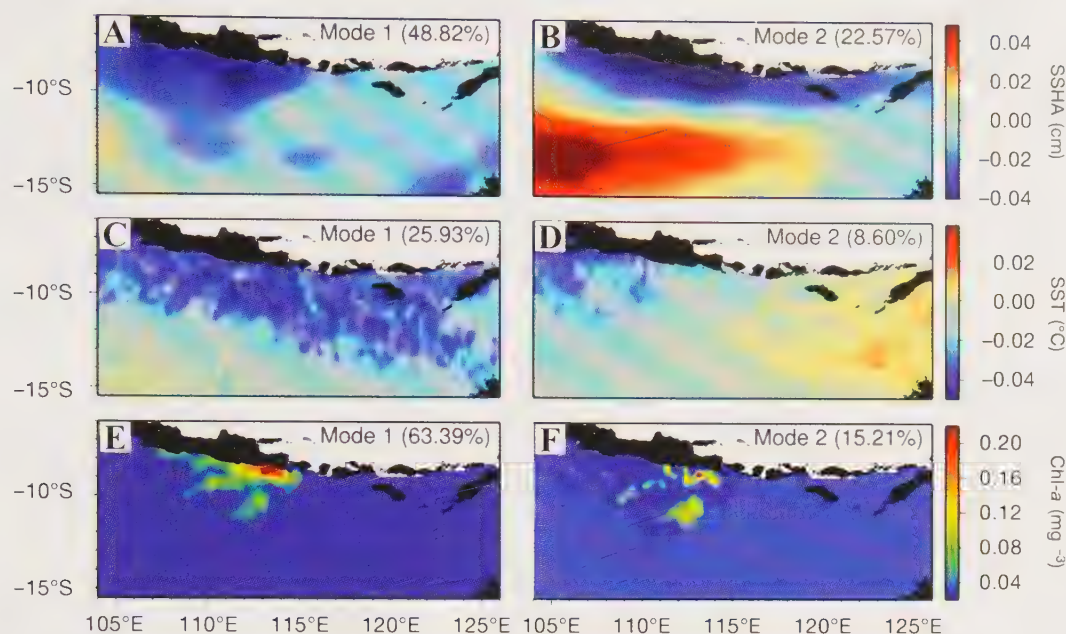


Figure 4

Spatial patterns of the empirical orthogonal function modes in the eastern Indian Ocean off Java from September 1997 to December 2000: (A) first mode of sea-surface-height anomaly (SSHA), (B) second mode of SSHA, (C) first mode of sea-surface temperature (SST), (D) second mode of SST, (E) first mode of chlorophyll-*a* (chl-*a*) concentrations, and (F) second mode of chl-*a* concentrations. Scale units are in centimeters, degrees Celcius, and milligrams per cubic meter for SSHA, SST, and chl-*a* data, respectively.

Spatial and temporal modes of ocean variability

The remote forcing in the timescale of interannual and seasonal variations due to ENSO and monsoons are represented by the first and second EOF modes of SSHA, SST, and chlorophyll-*a* concentrations, with the total energy variance from these 2 modes about 78.60% for chlorophyll-*a* values, 71.39% for SSHA, and 34.53% for SST (Table 1). The first spatial mode of SSHA contributed 48.82% of the total variance, indicating waters with relatively low temperatures and with negative SSHA concentrated along the southern coast of Java (Fig. 4A). The second spatial mode of SSHA contributed 22.57% of the total variance and showed that waters with relatively low temperatures were distributed along the southern coast of the Indonesian archipelago (Fig. 4B). The first spatial mode of SSHA corresponded with interannual variability, as shown by the first temporal mode (Fig. 5A). A map of the second spatial mode of SSHA clearly shows that this mode corresponded with seasonal variability, as indicated by the second temporal mode (Fig. 5B).

The SSHA results were associated with the first and second spatial modes of SST, with total variances of 25.93% and 8.60%, respectively. The first spatial mode of SST showed that waters with relatively low temperatures were concentrated along the southern coast of Java, extending to the offshore area (7–13°S) (Fig.

Table 1

Summary of the amplitude function (percentage of the total variability) of the first and second empirical orthogonal function modes of the sea-surface-height anomaly (SSHA), sea-surface temperature (SST), and chlorophyll-*a* (chl-*a*) concentrations in the eastern Indian Ocean off Java from September 1997 to December 2000.

Parameter	Mode 1 (%)	Mode 2 (%)	Total modes 1 and 2 (%)
SSHA	48.82	22.57	71.39
SST	25.93	8.60	34.53
Chl- <i>a</i>	63.39	15.21	78.60

4C). The second spatial mode of SST showed that those waters were spread along the western coast of Java (7–12°S), while waters with relatively high temperatures covered the eastern part of the EIO off Java (Fig. 4D). The amplitude function of the first mode of SST corresponded with interannual variability (Fig. 5C), and the second mode corresponded with the seasonal cycle in which the maximum and minimum SST occurred during the northwest monsoon (November–April) and southeast monsoon (May–October), respectively (Fig. 5D).

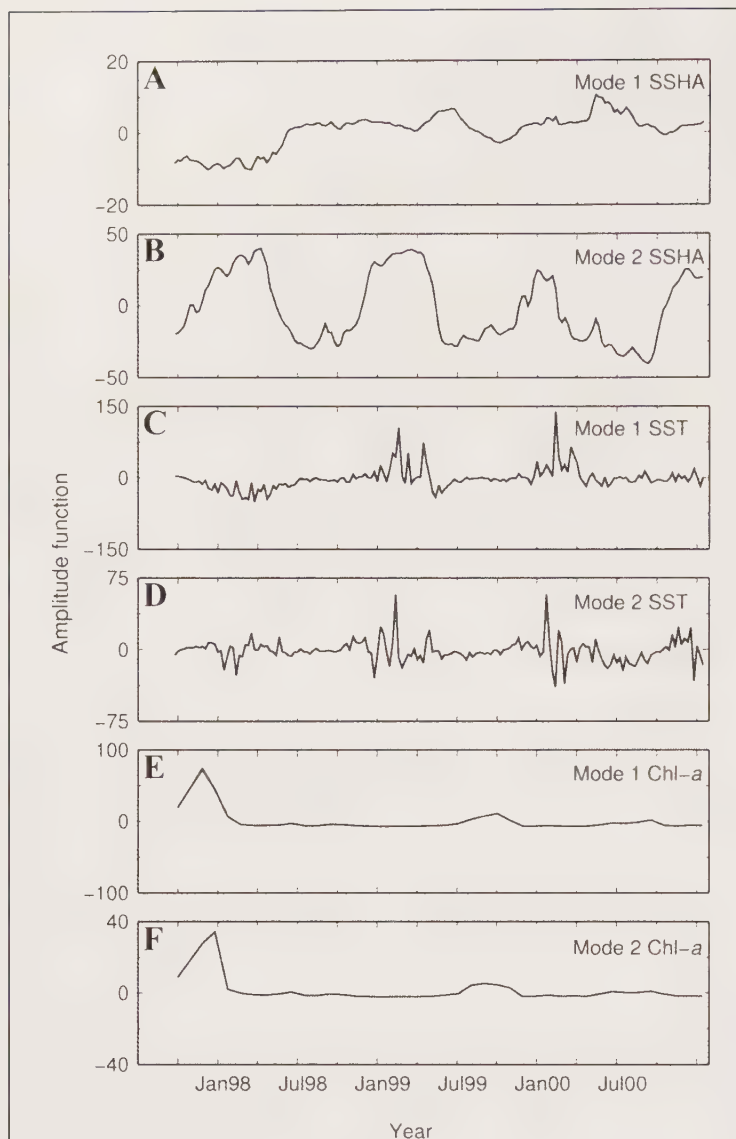


Figure 5

Amplitude function from the temporal mode of the analysis for the study area in the eastern Indian Ocean off Java from September 1997 to December 2000: (A) first mode of sea-surface-height anomaly (SSHA) (interannual signal), (B) second mode of SSHA (seasonal signal), (C) first mode of sea-surface temperature (SST) (interannual signal), (D) second mode of SST (seasonal signal), (E) first mode of chlorophyll-*a* (chl-*a*) concentrations (interannual signal), and (F) second mode of chl-*a* concentrations (annual signal). The x-axis represents the year, and the y-axis shows the amplitude function for each mode (nondimensional).

The first EOF mode of SSHA and SST showed an inverse relationship with the first EOF mode of chlorophyll-*a*, with a negative SSHA value and relatively low SST followed by higher chlorophyll-*a* concentrations along the southern coast of Java. The first mode of chlorophyll-*a* contained 63.39% of the energy

variance, and the second mode contributed 15.21% of the energy variance, with notably higher chlorophyll-*a* levels concentrated along the southern coast of Java (7–9°S). The amplitude function of the first mode of chlorophyll-*a* corresponded with interannual variability, and the second mode corresponded with the annual cycle. Positive values (chlorophyll-*a* concentrations greatly elevated above values seen in other periods) occurred during September–November 1997 (Fig. 5, E–F).

Generalized additive models

The results of the GAMs are presented as 1-parameter, 2-parameter, and 3-parameter models (Table 2). All of the variables used were statistically highly significant ($P < 0.0001$) for SSHA, SST, and chlorophyll-*a* concentrations. The addition of predictor variables at different levels resulted in an increase in the deviance in catch rates explained. In the 1-parameter models, SST explained the highest deviance (6.48%) and chlorophyll-*a* concentrations explained the lowest deviance (2.04%). The 3-parameter combination models explained the highest deviance (16.30%) and had the lowest AIC values.

GAM plots can be interpreted as the individual effects of predictor variables associated with SSHA, SST, and chlorophyll-*a* concentrations on Bigeye Tuna catch (Fig. 6, A–C). High probabilities of Bigeye Tuna presence were observed for SSHA ranging from –21 to 5 cm, for SST ranging from 24° to 27.5°C, and for chlorophyll-*a* levels ranging from 0.04 to 0.16 mg m⁻³. Negative effects on Bigeye Tuna were observed for SSHA >5 cm, SST values >27.5°C, and chlorophyll-*a* values of 0.01–0.03 mg m⁻³ and >0.16 mg m⁻³.

Spatial predictions for catch distribution of Bigeye Tuna were compared with the actual monthly fishery data collected during the El Niño (September and October 1997) and La Niña (March and April 1999) events. The predicted catch distribution of Bigeye Tuna in September 1997 during the El Niño event indicated a potential area with higher catch probability of approximately 70–80% at 10–16°S and 104–122°E, and the actual Bigeye Tuna fishing locations (with a HR of 0.41) occurred in the area between 12–16°S and 110–115°E (Fig. 7A). In October 1997, spatial predictions for catch distribution of Bigeye Tuna indicated locations with higher catch probability (60–70%) in the west at 7–12°S, 104–108°E and 14–16°S, 109–114°E, but the actual Bigeye Tuna fishing locations were located at 12–15°S, 110–116°E, where there was a predicted catch probability of around 20–40% and actual HR of only 0.20 (Fig. 7B). The

Table 2

Results from general additive models (GAMs) derived from catch rates of Bigeye Tuna (*Thunnus obesus*) in the eastern Indian Ocean off Java in 1997–2000 as a function of the oceanographic parameters ($N=2843$ samples). The best model was selected on the basis of the significance of predictor terms, reduction of Akaike's information criterion (AIC), and increase in cumulative deviance explained (CDE). SST=sea-surface temperature; SSHA=sea-surface-height anomaly; chl-*a*=chlorophyll-*a* concentrations estimated from SeaWiFS level-3 images (<http://oceancolor.gsfc.nasa.gov>).

Model		Variable	<i>P</i> value	AIC	CDE (%)
SST		SST	$<2.00 \times 10^{-16}***$	2117.04	6.48
SSHA		SSHA	$<2.00 \times 10^{-16}***$	2153.88	4.95
Chl- <i>a</i>		Chl- <i>a</i>	$<2.00 \times 10^{-16}***$	2219.38	2.04
SSHA	+	SSHA	$<2.00 \times 10^{-16}***$	2110.55	7.18
chl- <i>a</i>		Chl- <i>a</i>	$<2.00 \times 10^{-16}***$		
SST	+	SST	$<2.00 \times 10^{-16}***$	2065.54	9.20
chl- <i>a</i>		Chl- <i>a</i>	$<2.00 \times 10^{-16}***$		
SSHA	+	SSHA	$<2.00 \times 10^{-16}***$	1973.96	13.30
SST		SST	$<2.00 \times 10^{-16}***$		
SSHA	+	SSHA	$<2.00 \times 10^{-16}***$	1912.79	16.30
SST	+	SST	$<2.00 \times 10^{-16}***$		
chl- <i>a</i>		Chl- <i>a</i>	$<2.00 \times 10^{-16}***$		

***indicates statistical significance at the 0.001 level.

suspected shift in the distribution of Bigeye Tuna away from the fishing grounds caused the drop in the HR from 0.41 in September 1997 to 0.20 in October 1997.

During La Niña in 1999, spatial predictions indicated Bigeye Tuna catches with lower probabilities of 20–40% occurring in the offshore area of the western part of the EIO off Java. In March 1999, the spatial prediction of Bigeye Tuna catch (20–30%) was located around 12–16°S, 104–115°E, but actual Bigeye Tuna fishing locations were at 13–15°S, 106–107°E; 12–15°S, 109–112°E; and 12–13°S, 114–115°E (Fig. 7C). The spatial prediction of Bigeye Tuna catch (20–40%) moved to the west at 11–16°S and 104–111°E in April 1999 (Fig. 7D), but the actual Bigeye Tuna catch areas were located at 13–14°S and 11–15°S in the longitude range of 108–118°E.

Discussion

Catch rates of Bigeye Tuna varied over a range of time scales and apparently in relation to environmental changes. Changes in oceanographic conditions during ENSO events resulted in perceivable variations in Bigeye Tuna catches, with an average HR of 0.67 during the 1997–98 El Niño event. The 1999–2000 La Niña event, with an average HR of 0.44, was less favorable for catches.

The spatial patterns of the first and second EOF modes for SSHA, SST, and chlorophyll-*a* concentra-

tion gave typical negative SSHA, low SST, and high chlorophyll-*a* concentration along the southern coast of the Indonesian archipelago, and changes in these patterns could be exposed by the temporal mode as inter-annual variation related to the forcing of the 1997–98 El Niño event and upwelling evidence. Those typical spatial patterns are consistent with the oceanographic conditions during September–November 1997 (Fig. 3, A–C). The first and second modes of chlorophyll-*a* showed the characteristics of an upwelling pattern, with chlorophyll-*a* concentrations higher along the southern coast of Java than in other areas. Although it normally ends in October, upwelling was observed into November during the southeast monsoon in the El Niño event in 1997.

Our results are consistent with the findings of Sprintall et al. (1999) and Field et al. (2000), who reported that the ITF brings colder and warmer waters to the Indian Ocean during El Niño and La Niña events, respectively, and the local, alongshore winds south of Java are favorable for upwelling through December. They also confirmed that the upwelling signal could account for the reduced downwelling signal from the November Kelvin waves. In November 1997, Kelvin waves were not generated in the region and this condition caused the persistence of colder water along the southern coast of Java.

Chlorophyll-*a* concentrations contributed the highest energy variance, indicating that chlorophyll-*a* concentration was the main indicator of the forcing mechanisms responsible for the 1997–98 El Niño event. Our

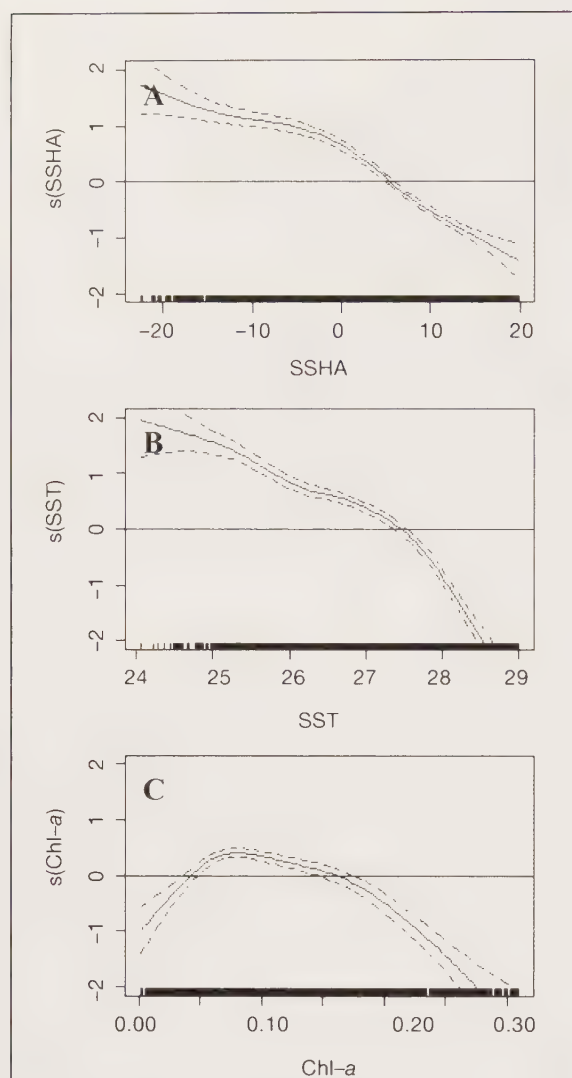


Figure 6

Effect of the 3 oceanographic variables—(A) sea-surface-height anomaly (SSHA), (B) sea-surface temperature (SST), and (C) chlorophyll-*a* (chl-*a*) concentrations—on Bigeye Tuna (*Thunnus obesus*) catches derived from generalized additive model (GAM) of presence-absence data. The x-axis shows the values of the explanatory variables, and the y-axis shows the results of smoothing the fitted values. The tick marks on the horizontal axis represent the values of the observed data points; the solid line indicates the fitted function. Dashed lines represent 95% confidence intervals. The horizontal line at zero indicates no effect. The percent frequency of occurrence was higher for all values for which the fitted GAM function was above the zero axis and lower for values <0.

anomalous high values of chlorophyll-*a* concentration observed in the EIO. Upwelling areas are potential convergence zones for plankton aggregation, attracting larger predators, such as tunas (Lehodey et al., 1997). Such concentrations of chlorophyll-*a* may cause the increased catches during El Niño event (Polovina et al., 2001; Lehodey et al., 2003; Polovina et al., 2004; Miller, 2007).

We used a binomial GAM to investigate the effects of environmental variables that affect the catchability of Bigeye Tuna. The effects of oceanographic conditions inferred from the GAM indicated that oceanographic factors strongly influence the catchability of Bigeye Tuna. SST was a more important oceanographic predictor of Bigeye Tuna catches than were the other environmental variables (SSHA and chlorophyll-*a*) in this region. Furthermore, this result from GAM analyses of SST indicates that remote forcing from the Pacific Ocean has a large effect on HR during an El Niño because of the reduction in heat transported from the Pacific to the Indian Ocean by the Indonesian Throughflow during El Niño events (Field et al., 2000; Gordon et al., 2010). Bigeye Tuna are very sensitive to changes in SST (Holland et al., 1992; Brill et al., 2005). Our results indicate that Bigeye Tuna catches increased in areas with relatively low temperatures (24–27.5°C) and decreased at temperatures >27.5°C (Fig. 6B). Our results are supported by previous research from the North Pacific Ocean, in which SST had the greatest effect on Bigeye Tuna at temperatures of 23–26.5°C (Howell et al., 2010).

SSHA was the second-most significant oceanographic predictor of Bigeye Tuna catch distribution in the EIO off Java. We used SSHA to understand oceanic variability, such as current dynamics, eddies, convergences, and divergences, which could be used as proxies for the potential location of tuna catches (Polovina and Howell, 2005). Our study showed that the preferred habitat for Bigeye Tuna was in the range of SSHA values of –21 to 5 cm (Fig. 6A). This finding indicates that Bigeye Tuna forage in areas of low and negative SSHA values in contrast to divergences in SSHA values. Howell and Kobayashi (2006) also found the presence of a strong gradient of sea-surface height in the region of Palmyra Atoll during the 1997–98 El Niño, coinciding with an increase in the geostrophic (subsurface) flow that may increase shoaling of longline sets. Negative SSHA would push the thermocline upward, nearer the surface, and the elevation of the thermocline would allow Bigeye Tuna from below to become more accessible to longline gear. This preferred condition may enhance the potential Bigeye Tuna habitat, as it apparently did during the 1997–98 El Niño, when increased Bigeye Tuna catches occurred. Our findings seem to agree with the results of Holland et al. (1992) and Brill (1994), who reported that Bigeye Tuna move toward cooler habitats to prevent overheating, with negative values of SSHA indicating that Bigeye Tuna are attracted only to shallow water when the thermocline is closer to the surface (Arizabalaga et al., 2008).

Among the 3 environmental predictors assimilated in the model, chlorophyll-*a* concentrations exhibited the

results are consistent with the work of Murtugudde et al. (1999), who showed that, in the Indian Ocean, intense El Niño events, such as the one in 1997–98, have direct effects on primary production and cause

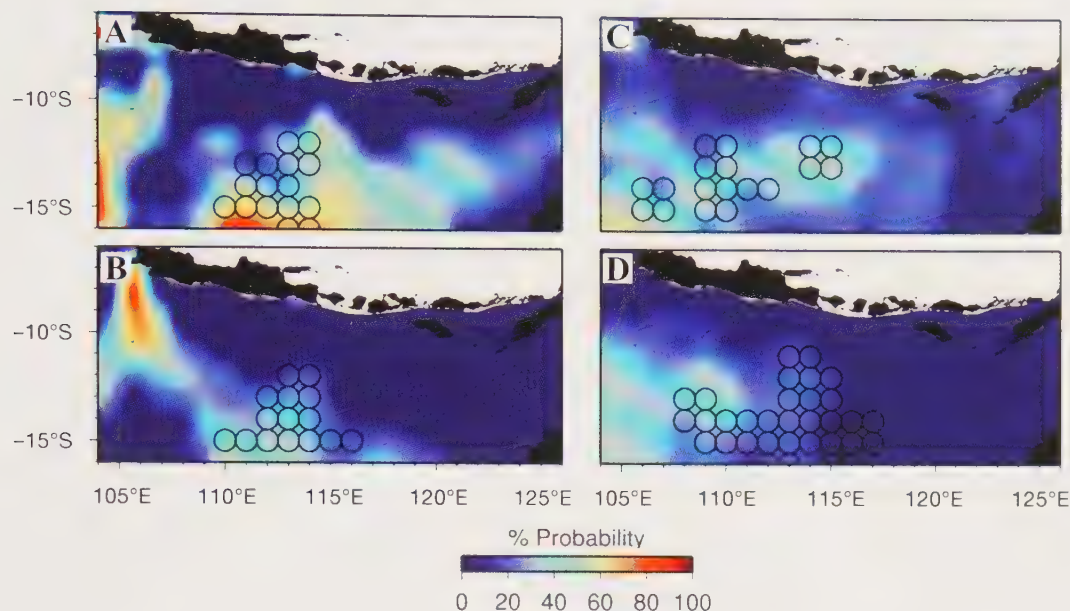


Figure 7

Spatial prediction for catch probabilities of Bigeye Tuna (*Thunnus obesus*) overlaid with actual fishing locations of Bigeye Tuna catch in the eastern Indian Ocean off Java for the El Niño event in (A) September 1997 and (B) October 1997 and for the La Niña event in (C) March 1999 and (D) April 1999. Color bars show the level of predicted catch probability of one or more Bigeye Tuna catches (0–100%); blue indicates the lowest catch probability (0), and red indicates the highest catch probability (100%). Circles outlined in black show the actual fishing locations for Bigeye Tuna catch (1° intervals). The original data set was gridded in 1° increments and smoothed for the purposes of better visualization.

lowest contribution to the model prediction. However, the derived relationship between this parameter and catches of Bigeye Tuna was statistically significant ($P < 0.0001$). Bigeye Tuna fishing sets were located in waters with relatively low-to-moderate chlorophyll-*a* values. Chlorophyll-*a* data is a valuable proxy for water mass boundaries and upwelling events. Overall, the GAM results showed that the distribution of Bigeye Tuna catch in the study area was influenced primarily by SST and SSHA. The lag time in food chain processes may explain the rather weak effect of chlorophyll-*a* concentration on HR.

Bigeye Tuna catchability could be influenced by many factors, in addition to oceanographic parameters, such as the depth range of longline sets, duration of longline operations, competition among gears, number of hooks, and experience level of the fishermen (Polacheck, 1991; Ward, 2008). In this study, the fishermen used the same fishing gear with similar fishing techniques. Therefore, we assumed that differences in fishing gear did not affect the catchability of Bigeye Tuna and we considered the number of hooks and environmental conditions to explain the catchability of Bigeye Tuna. Catchability fluctuated within and between years in relation to the number of hooks. During El Niño, high catchability coefficients occurred in May 1997 (1.56×10^{-7}) and June 1998 (1.47×10^{-7}),

coinciding with high HR of 0.94 and 0.83, respectively. This high coefficient number of catchability could be due to the higher number of hooks and catch of Bigeye Tuna during El Niño events related to oceanographic conditions favorable to Bigeye Tuna. The favorable oceanographic conditions were indicated by negative SSHA and by a colder SST than the normal condition of around 28–29°C. Marsac and Blanc (1999) reported that the anomalous upwelling conditions that occurred in the EIO, providing biological enrichment and a shallower thermocline, should have favored catchability in the purse-seine fishery for Bigeye Tuna during the 1997–98 El Niño. The catchability coefficient for November 2000 in our study appeared as an outlier. In that month, adverse weather conditions resulted in a decreased number of hooks and a lower HR; the increased catchability may have been due to the reduced fishing competition among longliners.

The favorable oceanographic conditions for Bigeye Tuna catches during El Niño resulted in increasing predicted catch probabilities for Bigeye Tuna. The predicted distribution of Bigeye Tuna catch during El Niño showed a potential area with higher catch probability compared with catch probability for La Niña events. Between the El Niño and La Niña events, fishing effort within the fishing grounds did not shift as much as did the predicted tuna habitat. Most catches

were made in the area of lower catch probabilities; however, some were from the boundary regions of high probability in the offshore waters of Java. Predictions of higher catch probabilities of Bigeye Tuna catches appeared to be associated with frontal areas in 10–12°S, a region that seemed to reveal the importance of the confluence on the eastward IOKW and SJC that met with the outflow of the ITF and SEC in the offshore area of the EIO off southern Java.

There were many potential fishing locations that were not used optimally, and this inefficient use reduced the total catch to much less than the level that was expected during the El Niño 1997–98 year. Nonetheless, the catch remained significantly higher during this El Niño event than during the 1999–2000 La Niña event. The mismatch between optimal fishing locations and actual fishing locations can be attributed to one or more of the reasons outlined below:

The fishermen did not have the capability to determine potential Bigeye Tuna habitats on the basis of large-scale regional shifts in oceanographic and climate regimes. They still used traditional methods, such as targeting locations similar to the ones where they had previously found Bigeye Tuna.

The cost of fuel limited how far the fishermen could travel in search of Bigeye Tuna. Their fishing ground covered the area around 10–16°S and 108–120°E, the same region used in our data analysis.

The fishermen did not target other species when fewer Bigeye Tuna were caught. They caught other species, such as small pelagic fishes (*Sardinella* sp. or *Euthynnus* sp.), only for their own consumption during fishing trips (not as main targets). Therefore, we assumed that other catches did not influence the fishing effort.

Political or management boundaries were not major problems facing this traditional fishing ground. Instead, the main constraints were the financial limits on long or distant fishing operations and the rapid fluctuations in fuel costs from week to week. The price of Bigeye Tuna depends on these factors: the location in which it is caught (fish caught farther from market are more expensive), the season (during the northwest monsoon, when fish abundance decreases, the price increases), and climate variability that affects environmental conditions (during El Niño event, fish generally are abundant and the price drops, and vice versa during La Niña event).

Conclusions

This study has shown the effects of ENSO-induced oceanographic conditions on catch rates of Bigeye Tuna in the EIO off Java. Spatiotemporal patterns in oceanographic conditions shown by the EOF, combined with the results of the GAMs, indicate that the 1997–98 El Niño event had a positive effect on catch rates of Bigeye Tuna in the EIO off Java.

The EOF modes further highlight that interannual and seasonal time scales are the main factors that affect ocean current variability in the study area. The EOF analysis also provides evidence for the effects of the 1997–98 El Niño event in the EIO off the southern coast of Java—the dominant features being negative SSHA, cold SST, and high chlorophyll-*a* concentrations. In terms of these environmental variables, the binomial GAM confirmed that SST was the major factor that influenced Bigeye Tuna catches. These results indicate that the use of a GAM with 3 predictor variables may facilitate the identification of areas with potentially high Bigeye Tuna catch in the EIO off Java.

Our results show significant effects of ENSO on Bigeye Tuna catches. For example, favorable oceanographic conditions corresponded with the El Niño event, as indicated by the EOF and GAM analyses. We did not consider depth range data for Bigeye Tuna catches. Further investigations into prediction of fishing ground locations through the use of long-term, historical time series of environmental conditions and fishing efforts—fishery data sets of greater spatial and temporal resolutions than the data sets used in our study—are needed to better understand the effects of climate variability and fishing effort on changes in Bigeye Tuna catches in the EIO off Java.

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Abstract—We monitored the movements of 45 adult Summer Flounder (*Paralichthys dentatus*) between June 2007 and July 2008 through the use of passive acoustic telemetry to elucidate migratory and within-estuary behaviors in a lagoon system of the southern mid-Atlantic Bight. Between 8 June and 10 October 2007, fish resided primarily in the deeper (>3 m) regions of the system and exhibited low levels of large-scale (100s of meters) activity. Mean residence time within this estuarine lagoon system was conservatively estimated to be 130 days (range: 18–223 days), which is 1.5 times longer than the residence time previously reported for Summer Flounder in a similar estuarine habitat ~250 km to the north. The majority of fish remained within the lagoon system until mid-October, although some fish dispersed earlier and some of them appeared to disperse temporarily (i.e., exited the system for at least 14 consecutive days before returning). Larger fish were more likely to disperse before mid-October than smaller fish and may have moved to other estuaries or the inner continental shelf. Fish that dispersed after mid-October were more likely to return to the lagoon system the following spring than were fish that dispersed before mid-October. In 2008, fish returned to the system between 7 February and 7 April. Dispersals and returns most closely followed seasonal changes in mean water temperature, but photoperiod and other factors also may have played a role in large-scale movements of Summer Flounder.

Migratory and within-estuary behaviors of adult Summer Flounder (*Paralichthys dentatus*) in a lagoon system of the southern mid-Atlantic Bight

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The continued degradation of estuarine environments associated with eutrophication, shoreline development, and global climate change necessitates a better understanding of how seasonal residents, like Summer Flounder (*Paralichthys dentatus*), use mid-Atlantic estuaries (Gibson, 1994; Beck et al., 2001). Estuaries provide juvenile and adult Summer Flounder with the water temperatures, food resources, and protection from predation that are necessary for their growth and survival (Stierhoff et al., 2006). Summer Flounder migrate offshore in the fall and winter to spawn over the outer continental shelf before they migrate back inshore the following spring, often returning to the same estuary in subsequent years (Sackett et al., 2007). As a result, stock abundance is influenced by local estuarine conditions (Ray, 2005). The use of estuaries as nursery habitat by Summer Flounder and the responses of juvenile Summer Flounder to estuarine conditions have been extensively examined (e.g., Malloy and Targett, 1994; Tyler, 2004;

Necaise et al., 2005; Stierhoff et al., 2006, 2009). Only recently, however, have migratory and within-estuary behaviors of adult Summer Flounder been examined (Sackett et al., 2007, 2008; Henderson, 2012).

Migration timing traditionally has been determined through assessment of the abundance of fishes in an estuary over time with standard fisheries methods, such as bottom trawl surveys. However, population-level monitoring is insufficient to understand the dynamics of emigration or the variation in individual responses (DeCelles and Cadrin, 2010). In recent years, acoustic telemetry has been established as a powerful tool for observation of individual variability in behaviors (Heupel et al., 2006; DeCelles and Cadrin, 2010). A study of acoustically monitored adult Summer Flounder in the Mullica River–Great Bay estuary in New Jersey (located in the northern mid-Atlantic Bight [MAB]) indicated that a large number of fish departed the estuary in July, but the precise timing varied between years (Sackett et al., 2007).

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Therefore, variation in emigration timing may exist not only by latitude but also among individual fish within a system. Some adult Summer Flounder have been known to return to the same estuary in subsequent years (Poole, 1962; Sackett et al., 2007; Henderson, 2012), but factors that influence site fidelity in Summer Flounder are not well understood.

Acoustic telemetry has also been used to identify variations in Summer Flounder within-estuary activity. For example, Summer Flounder in the Mullica River–Great Bay estuary primarily used the lower bay (near the inlet), but some fish resided in other areas (Sackett et al., 2008). Likewise, most fish remained in the Mullica River–Great Bay estuary until emigration to the outer shelf, but several adults exited and entered the system multiple times (i.e., exhibited temporary emigration). Similar patterns were observed in the Chesapeake Bay (southern MAB), where some adults remained sedentary and resided at structured sites for long periods of time, and others were more active and traveled long distances (Henderson, 2012).

The continuation of acoustic studies is necessary to identify similarities and differences in behavioral patterns between regions and to investigate the drivers behind these patterns. Our objectives for this study were to use acoustic telemetry to describe the migratory and within-estuary behaviors of adult Summer Flounder from a previously unstudied lagoon system in the southern portion of the MAB. The lagoon systems off Virginia's Eastern Shore are subject to large fluctuations in temperature typical of most MAB systems (0–30°C), but they differ from larger estuaries in that they are shallow (mean depth <3 m), well-mixed, and polyhaline areas. These lagoon systems are a nursery ground for juvenile Summer Flounder (Schwartz, 1964; Norcross and Wyanski, 1994; Desfosse, 1995; Kraus and Musick, 2001), but they also support a large number of adults and an active recreational fishery (Richards and Castagna, 1970). Previous descriptions of the use of our chosen lagoon system by Summer Flounder have been limited to descriptions of juvenile habitat preferences (Wyanski, 1990; Norcross and Wyanski, 1994) and adult migration patterns determined by traditional mark-recapture methods (Kraus and Musick, 2001; Desfosse, 1995).

We used the data from our acoustic telemetry study to determine 1) dispersal and return rates, 2) duration of residency, 3) spatiotemporal distribution, and 4) activity of fish within the system. Because tidal stage, time of day, and temperature all have been associated with flatfish activity (Olla et al., 1972; Casterlin and Reynolds, 1982; Wirjoatmodjo and Pitcher, 1984; Malloy and Targett, 1991; Szedlmayer and Able, 1993; Henderson, 2012), these factors were considered in our examination of within-estuary activity. We also analyzed the effects of seasonal temperature, photoperiod, and fish size on dispersal, returns, and residency times (Smith, 1973; Able and Kaiser, 1994).

Materials and methods

Study site

The estuarine lagoon system near Wachapreague, Virginia, resides behind a series of low barrier islands and primarily connects with the Atlantic Ocean through Wachapreague Inlet (Fig. 1). The 2 main channels leading from Wachapreague Inlet divide into smaller channels that cut through marsh areas (dominated by smooth cordgrass [*Spartina alterniflora*]) before they open into large, shallow tidal flats. Channels were identified as areas ~3–12 m deep, and tidal flats were identified as areas <3 m deep. As with most seaside lagoon systems in Virginia, the system near Wachapreague is characterized by restricted access to the ocean, minimal freshwater input, and a moderate tidal range (1.2–1.4 m; NOAA Center for Operational Oceanographic Products and Services, <http://tidesandcurrents.noaa.gov/tides07/tab2ec2b.html#44>). Strong currents are typical because of natural constrictions at the inlet and in the channels (Conrath, 2005), although currents generally dissipate with distance from the inlet. Sediment type follows the energy gradient, with coarse sand within and near the inlet, and progressively finer (muddy) sediments at greater distances from the inlet (Wyanski, 1990).

We divided our study area into 4 regions (Fig. 1):

- 1 Wachapreague Inlet—the primary point of ingress and egress of fish characterized by depths of 6–15 m and strong currents; the inlet is about 625 m wide.
- 2 Upper channels—the channel leading north from Wachapreague Inlet and its divergent channels.
- 3 Lower channels—the channel leading south from Wachapreague Inlet and its divergent channels.
- 4 Tidal flats (also known locally as *bays*)—the shallowest bodies of water included in our study. Although several tidal flats are present in this area, only Swash Bay was included in our study area because we could monitor the movements of Summer Flounder into and out of this area.

We recorded environmental conditions in the inlet, channels, and tidal flat from 8 June 2007 to 29 July 2008 with 3 YSI 6920-O¹ multiparameter water-quality sondes (YSI, Inc., Yellow Springs, OH; Fig. 1), which recorded temperatures and dissolved oxygen concentrations once per hour. Sondes were replaced with calibrated units every 1–2 weeks in the summer and (as fouling diminished) every 2–4 weeks thereafter. Erroneous recordings due to membrane fouling, battery failure, and calibration drift were removed from the data set. Data from the water-quality sondes confirmed that dissolved oxygen concentrations generally remained above the critical oxygen level (27.2%, 2.0 mg O₂ L⁻¹) for adult Summer Flounder at typical summer bottom-water

¹ Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.



Figure 1

(A) The distribution of acoustic receivers and water-quality sondes installed in the Wachapreague lagoon system for this study of Summer Flounder (*Paralichthys dentatus*) behaviors between June 2007 and July 2008. The location of the Wachapreague lagoon system in the southern mid-Atlantic Bight is shown by the square in the smaller map. Regions specified in the text are Wachapreague Inlet, upper channels, lower channels, and tidal flat. Receivers S3, S5–S9, S11, and S12 provided supplemental data on the activity in regions outside of our study area. (B) In this map of acoustic receivers, each circle represents the approximate detection range (radius=350 m) of the receivers deployed in the Wachapreague lagoon system.

temperatures (Capossela et al., 2012). Photoperiod (i.e., day length) was acquired from tide prediction software (Jtides, vers. 4.9; <http://www.arachnoid.com/JTides>).

Telemetry and tagging

On 22 May 2007, 50 Summer Flounder (261–558 mm total length [TL]) were captured at the study area by hook and line, identified from Murdy et al. (1997), and immediately anesthetized with 60 mg L⁻¹ AQUIS (AQUI-S New Zealand Ltd., Lower Hutt, New Zealand) to allow surgical implantation of individually coded 69-kHz transmitters (V9-2L-R64K; VEMCO Division, AMIRIX Systems, Inc., Bedford, Canada) by using established procedures (Fabrizio and Pessutti, 2007). Transmitters were 30 mm long and 9 mm in diameter and had a delay time of 60–180 s and a projected 14-month battery life. All fish were tagged and

released in the upper channels with the exception of a single fish that was captured, tagged, and released on the tidal flat. Before release, all fish were allowed to fully recover in an onboard aquarium that accommodated total length, and externally tagged with an individually numbered T-bar anchor tag inserted near the caudal peduncle to alert anglers to report recaptures. We considered all fish to be adults because Summer Flounder can reach maturity at 240–300 mm TL (Morse, 1981).

Summer Flounder migratory and within-estuary behaviors were examined from 8 June 2007 until the last fish departed on 17 January 2008. We chose the start date (8 June 2007), which was approximately 2 weeks after the release of tagged fish, to limit the influence of any atypical activity patterns due to recovery from capture and surgery (Knights and Lasse, 1996; Rogers and White, 2007). We recorded fish locations with 31

receivers (VR2, VR2W; VEMCO) deployed throughout the study area (Fig. 1A). Most receivers were deployed by 8 June 2007 (receivers numbered 1–27), but 4 receivers were deployed on 26 June (receivers numbered 28–30) and 16 July (receiver numbered 31) to provide additional coverage. Receivers were attached to an anchored line fitted with a buoy and positioned near the bottom of the water column (≤ 1 m from the bottom of the ocean floor) with the hydrophone oriented downward. Range tests conducted throughout the study area indicated an approximate detection range of 350 m.

We placed as many receivers as possible ~700 m apart in the upper and lower channels to be able to monitor fish movements on the scale of 100s of meters (Fig. 1B). Currents and boat traffic limited the placement of receivers in certain locations in the upper channels and prevented the use of a directional gate (Heupel et al., 2006) at Wachapreague Inlet. In these cases, receivers were placed in the next suitable location. The tidal flat was too shallow for extensive receiver coverage; instead, we used receivers to monitor fish as they entered and exited the tidal flat. Most receivers were retrieved on 31 January 2008, but 12 receivers (receivers numbered 5–7, 16–18, and 22–27; Fig. 1A) were left in the system to detect fish returning to the Wachapreague system the following year. To prevent receiver loss, we began retrieval of the receivers that were farthest from the inlet in mid-April. All receivers were retrieved by 29 July 2008.

A separate acoustic telemetry study conducted by researchers to examine movements of Cownose Ray (*Rhinoptera bonasus*) in the Wachapreague system overlapped with the timing of our Summer Flounder study. Receivers from the Cownose Ray study were placed mostly in small channels far from Wachapreague Inlet in an area not covered by our receivers. Receivers for that study were deployed on 26 June 2007 (receiver labeled S3) and 26 July 2007 (receivers labeled S5–S9, S11–S12; Fig. 1A) and retrieved on 17 November 2007. The receivers in the Cownose Ray study were spaced too far apart to meet the specific objectives of our study and detections from these receivers were not used in our analyses. We did note, however, the extent to which Summer Flounder were detected in these small back channels and henceforth refer to these receivers as *supplemental receivers*.

Migratory behaviors

Data were examined over weekly intervals to examine patterns of seasonal migration. We considered a fish to have dispersed on the last day it was detected at or near Wachapreague Inlet (receivers 17–22, 31; Fig. 1A). Likewise, we considered a fish to have returned when it was first redetected at Wachapreague Inlet or within the lagoon system. Weekly probabilities of dispersal and return were calculated with the Kaplan-Meier estimator, a nonparametric approach that requires no assumptions about the underlying hazard function

and accommodates censored fish (Pollock et al., 1989; Bennetts et al., 2001). Fish were censored from (i.e., not included in) this analysis if they were no longer detected but did not depart from the system through Wachapreague Inlet; the fate of such fish could not be conclusively determined. Censored fish may have resided in the system undetected, been removed by fishermen or predators, or have left the system through another route.

We used a piecewise linear regression model to identify when dispersal rates changed (i.e., the *change-point*), and we fitted the model to the data with non-linear least-squares estimation (the NLIN procedure in SAS, vers. 9.2, SAS Institute, Inc., Cary, NC; e.g., Ryan et al., 2007). The time before dispersal rates changed was considered the *residency period*, a time during which most fish were found within the lagoon system. The time after dispersal rates changed was considered the *emigration period*, during which most fish were observed finally to have dispersed. We classified fish according to observed migratory behaviors: those fish that dispersed early (during the residency period) and those fish that dispersed late (during the emigration period). An odds ratio (Agresti, 2007) was used to test the association between the timing of dispersal (i.e., residency period vs. emigration period) and the likelihood that a fish would return to the Wachapreague system the following year.

Some fish were detected at or near the inlet (receivers 17–22, 31) but were subsequently undetected for 14 or more consecutive days before redetection. These fish were classified as *temporary emigrants* because they were presumed to have exited and re-entered the lagoon system. Such behaviors were consistent with activity reported in a previous study (Sackett et al., 2007). Tagged fish, including temporary emigrants, were considered residents until final dispersal out of the inlet, and residence time was defined as the total number of days from the start of our study (8 June 2007) until the last detection at or near the inlet before final dispersal. The residence time of uncensored fish was used to calculate a mean residence time for Summer Flounder in the Wachapreague system. The mean residence time reported throughout this article is, therefore, an estimate of least (minimum) residence time because we do not know how long tagged fish were present in the lagoon system before the start of our study. Mean residence time and other mean values are reported as mean ± 1 standard error.

The effects of mean monthly temperature and mean monthly photoperiod on the percentage of fish that finally dispersed in a given month (log-transformed to improve homogeneity of variance) were examined with a multiple linear regression (general linear model [GLM] procedure in SAS). We also examined the effect of fish size on the probability of final dispersal before and after dispersal rates changed with logistic regression (LOGISTIC procedure in SAS). Goodness-of-fit sta-

Table 1

The total detectable area (km²) that we monitored for the presence of Summer Flounder and the percentage of the total detectable area in each defined region (upper channels, lower channels, tidal flat, and inlet) of the Wachapreague lagoon system, on the basis of a 350-m detection range, for this study of Summer Flounder (*Paralichthys dentatus*) behaviors. Also included are the proportions of time Summer Flounder spent in each region and the proportions of fish found in each region over the residency and emigration periods (8 June 2007–17 January 2008). The sum of the proportion of fish that used each region exceeds 1 because a single fish could occupy more than 1 region over the study period.

Region	Detectable area (km ²)	Percentage of total area (%)	Total mean proportion of time (%)	Total proportion of fish (%)
Upper channels	2.75	39.2	78.1	97.8
Lower channels	2.21	31.5	19.4	28.9
Tidal flat	1.29	18.5	0.4	4.4
Inlet	0.76	10.8	2.1	67.7
Total area	7.01			

tistics were calculated to assess the fit of the model through the use of the LOGISTIC procedure in SAS.

Within-estuary behaviors

We ascertained the temporal and spatial distributions of Summer Flounder in the upper channels, lower channels, tidal flat, and Wachapreague Inlet by examination of monthly distributions of Summer Flounder until all fish finally dispersed. Because the total detectable area that we monitored for the presence of Summer Flounder varied between regions (Table 1), our assessment of fish activity by region did not rely on continuous detection. We calculated the proportion of fish in each region by month as the number of fish detected in a region divided by the total number of fish present in the system that month. We also calculated the proportion of time the average fish resided within a region each month as the total time a fish spent in a region divided by the total time spent in all regions that month. Time in a region was defined as the total time between the first and last detection before detection in another region; receivers provided sufficient coverage to monitor fish movement into and out of the 4 regions (Fig. 1B). For fish that moved between regions, we did not use the length of time between the last region-specific detection and the next region-specific detection because we could not objectively assign fish location during that interval to a specific region. Because not all fish could be assigned objectively to a region each month, the sum of the proportions of fish using each region could be <1 for a given month. Conversely, the sum of the proportions of fish using each region could be >1 because a single fish could occupy more than one region in any given month. In addition to monthly analyses, we calculated the proportions of fish present and time spent in each region for the

residency and emigration periods. The z statistic was used to test for differences in the mean proportions between the residency and emigration periods (Fleiss, 1981). All proportions were expressed as percentages.

We used movement between receivers to calculate the activity index, which we defined as the total number of times an individual moved between receivers during nonconsecutive 6-h periods. We limited the data to fish in the upper channels during the residency period because the sample size was highest in this location and during this time (8 June 2007 to 10 October 2007; see the *Results* section). For each 6-h period, we assigned an activity index value of zero when a fish did not move between receivers, and a value of 1 for each arrival at a different receiver (adjacent or non-adjacent). The activity index was weighted to account for variation in distances between receivers (rounded to the nearest integer) and summarized weekly for individual fish by tidal stage (ebb, slack before ebb, flood, and slack before flood) within each time-of-day interval (day or night). Day (10:00–16:00) and night (22:00–4:00) were restricted to these nonconsecutive 6-h periods to minimize autocorrelations associated with successive observations on the same fish during day and night periods (Rogers and White, 2007). We also computed mean temperature for each period (tidal stage, time of day, and week combination).

We examined the relationship between activity indices and week, time-of-day, tidal stage, and temperature with a generalized repeated measures model (GENMOD procedure in SAS). This equation represents the statistical model fitted to the data:

$$\log(\lambda_{ijk}) = \mu + \alpha_i + \delta_j + \tau_k + \gamma_i$$

where λ_{ijk} = the mean activity in week i , time of day j , and tidal stage k ;

μ = the overall mean activity;

α = the week effect ($i=1, 2, 3, \dots, 32$);
 δ = the time-of-day effect ($j=\text{day, night}$);
 τ = the tidal stage effect ($k=\text{ebb, flood, slack before ebb, and slack before flood}$); and
 γ = the effect of mean temperature.

All effects in this model were considered fixed. All plausible interactions (temperature $\times$ tidal stage, temperature $\times$ time of day) were investigated and found to be insignificant ($\alpha=0.05$). We modeled the repeated measures of activity (discrete count data) as a negative binomial response after verification of the superior fit of the negative binomial distribution to the Poisson distribution to these data. According to the quasi-likelihood information criterion (a modification of Akaike's information criterion applied to models fitted by generalized estimating equations; Littell et al., 2006), the independent correlation matrix best described the nature of the correlation among repeated measurements within subjects. This correlation matrix is the simplest covariance model, where the within-subjects correlation is zero (Littell et al., 2006).

Results

Migratory behaviors

The fish included in all subsequent analyses were the fish that were alive and detected at receivers as of 8 June 2007. As a result, 45 out of 50 tagged fish were included in the analyses (278–558 mm TL). Of the 5 fish we eliminated, 1 was assumed dead (all detections were at a single receiver). Another fish departed through the inlet before 8 June 2007 and was subsequently detected in Delaware Bay (~100 km to the north) on 9 June 2007 (Fox²). The remaining 3 fish were never detected by our receivers, and we assume these fish either departed undetected or were harvested by recreational anglers but not reported. All except 1 of the 45 fish included in the analyses were detected in June; the remaining fish was detected for the first time in July. Most tagged individuals accounted for <6% of the total number of detections, which was 165,003. Two fish, however, contributed 24% and 13% of the total detections. These individuals were detected continuously at receivers for long periods of time with few gaps between detections.

The mean residence time for Summer Flounder in the lagoon system was 130 ± 13 days, or about 4.3 months (range: 18–223 days). Fish dispersed throughout the study period, but dispersal rates increased significantly after mid-October [change-point=week 18 (11 October 2007); $F=212.2$, $P<0.05$; Fig. 2]. On the basis of the Kaplan-Meier estimator, only 27% of tagged Summer Flounder had dispersed by 10 October 2007. Accordingly, the period from 8 June 2007 to 10 October 2007 was identified as the residency period (Fig. 2); the majority of fish that dispersed during this period did so shortly after they were tagged in June (Fig. 3). June was also the month with the highest number of censored fish (i.e., fish of unknown fate; Fig. 3). The emigration period was identified from 11 October 2007 to 17 January 2008, when the last fish departed (Fig. 2). During this period, dispersal rates increased such that 50% of fish departed by 11 November 2007, although most fish (31%) dispersed in December. Only 7 fish were classified as temporary emigrants, remaining undetected for 14 or more consecutive days (range: 14–154 days) after detection near the inlet and before redetection in the system and subsequent final dispersal.

Between 7 February and 7 April 2008, 17 Summer Flounder (36%) returned to the lagoon system (Fig. 2). Four of these fish did not disperse through Wachapreague Inlet in 2007, and, therefore, their dispersal dates were unknown. Of the returning fish with known dispersal dates, 58% (11 individuals) dispersed during the emigration

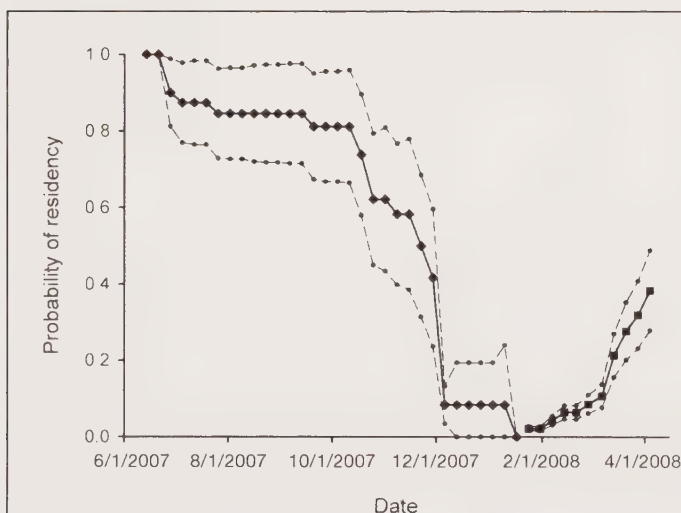


Figure 2

The probability that tagged Summer Flounder (*Paralichthys dentatus*) resided in the Wachapreague lagoon system from June 2007 to April 2008 on basis of the Kaplan-Meier estimator (solid lines) with 95% confidence intervals (dashed lines). Dispersal of tagged fish (◆) was monitored from 8 June 2007 until the last fish emigrated on 17 January 2008. Dispersal rates changed significantly after 11 October 2007 (change-point). The time before the change-point was considered the residency period, a time during which most fish remained within the lagoon system. The time after the change-point was considered the emigration period, during which most fish were observed dispersing from the Wachapreague lagoon system. Returns of tagged fish (■) were monitored from 18 January 2008 to 29 July 2008. The last return was detected on 7 April 2008.

² Fox, D. 2007. Personal commun. Delaware State Univ., 1200 N. DuPont Highway, Dover, DE 19901.

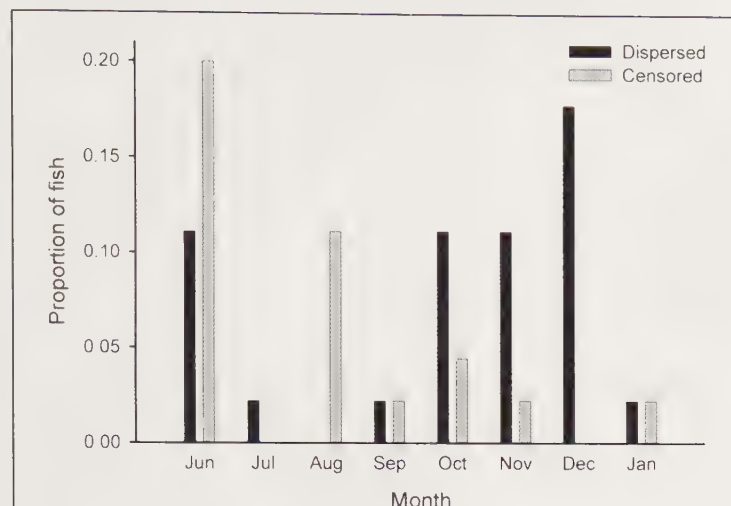


Figure 3

The proportion of Summer Flounder (*Paralichthys dentatus*) in each month from June 2007 to January 2008 that dispersed or was censored. Censored fish were fish that did not disperse through Wachapreague Inlet but were no longer detected by our acoustic receivers and had unknown fates. Total monthly sample sizes were 45 (Jun), 31 (Jul), 30 (Aug), 25 (Sep), 23 (Oct), 16 (Nov), 10 (Dec), and 2 (Jan).

period and 29% (2 individuals) dispersed during the residency period. Consequently, the odds of returning to the lagoon system were 3.5 times greater for fish that departed during the emigration period than for fish that departed during the residency period (odds ratio=1.4/0.4). It is possible that other fish returned undetected to the Wachapreague system because of the limited number of receivers in the system between February and July 2008; however, returning fish likely re-entered the system through the inlet and were detected by our receivers.

The emigration period was characterized by a larger seasonal variation in water temperature than that observed for the residency period (coefficient of variation [CV]_{residency}=9.5%, CV_{emigration}=46%). Dispersal followed the steep decline in temperature more closely than it did the gradual shift in day length, which (in contrast to changes in water temperature) was smooth and almost constant over time (CV_{residency}=7.7%, CV_{emigration}=5.8%; Figs. 4, 5). The multiple linear regression that included both temperature and photoperiod as predictors of dispersal was significant ($F=20.3$, $P<0.05$) and explained 89% of the variation in monthly dispersals. Temperature was a significant predictor of mean percent disper-

sal ($F=6.39$, $P=0.05$), but photoperiod was not ($F=0.94$, $P=0.38$). The length of time over which we observed returning fish (3 months) was inadequate to statistically examine the effects of mean monthly temperature and photoperiod on the timing of return.

The mean sizes at tagging for fish that dispersed during the residency and emigration periods were 437 ± 21 mm TL and 367 ± 13 mm TL, respectively. We found that the timing of dispersal was inversely related to fish size at the time of tagging ($\chi^2=8.45$, $P<0.05$). Larger fish were more likely to leave the system during the residency period (before October 11) than were smaller fish. Conversely, smaller fish were more likely to disperse during the emigration period. The goodness-of-fit of this model indicated that predicted and observed frequencies were not significantly different ($\chi^2=3.86$, $P=0.80$), indicating the adequacy of the logistic regression model as a descriptor of these data.

Within-estuary behaviors

Summer Flounder primarily used the upper channels during the residency period, although fish were detected in all habitats (Fig. 6, A and B). Fish occupied the upper and lower channels for 78% and 19%, respectively, of the total time that fish were detected (Table 1). With the exception of the single fish released in the tidal flat, all fish were

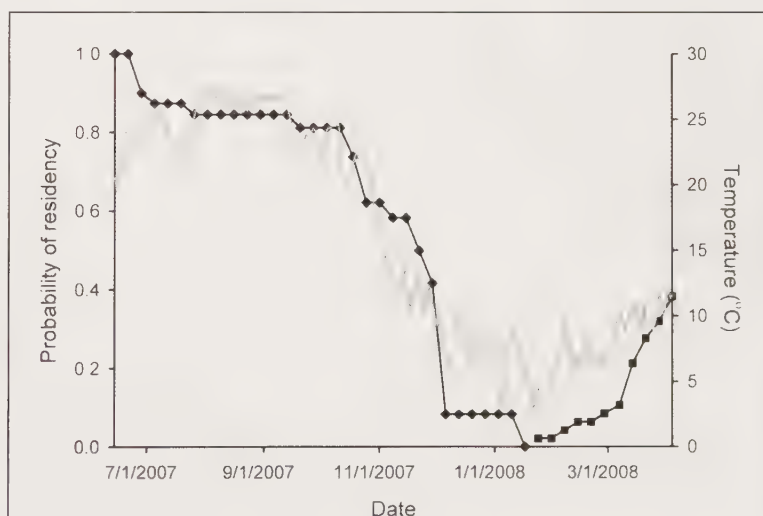


Figure 4

The proportion of Summer Flounder (*Paralichthys dentatus*) that dispersed from (◆) and returned to (■) the Wachapreague lagoon system from 8 June 2007 to 7 April 2008 (when the last fish was detected returning), on the basis of the Kaplan-Meier estimator. Mean daily temperature (°C; gray line) is also plotted. Confidence intervals have been omitted for clarity.

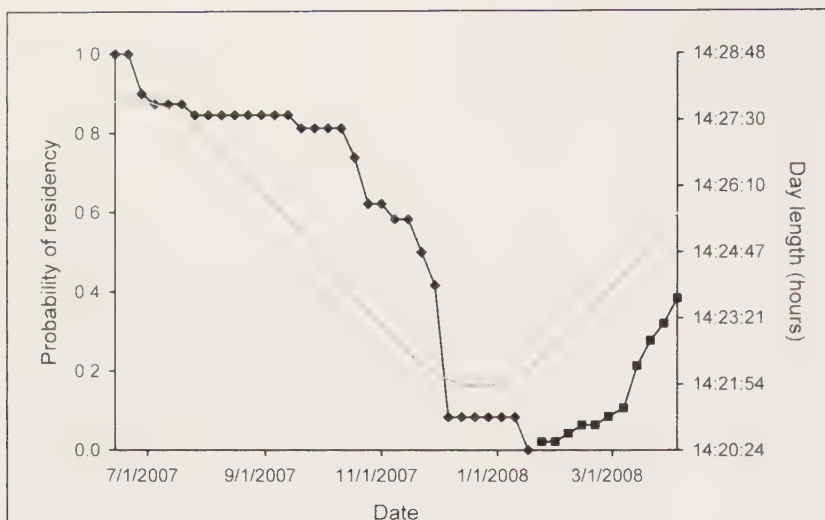


Figure 5

The proportion of Summer Flounder (*Paralichthys dentatus*) that dispersed from (◆) and returned to (■) the Wachapreague lagoon system from 8 June 2007 to 7 April 2008 (when the last fish was detected returning), on the basis of the Kaplan-Meier estimator. Photoperiod (day length in hours; gray line) is also plotted. Confidence intervals have been omitted for clarity.

detected in the upper channels, but only 27% (12 individuals) of the fish that were detected in the upper channels were also detected in the lower channels. This finding indicates that the majority of fish released in the upper channels (73%, 32 individuals) remained near the release site in the upper channels until dispersal.

The proportion of time and the proportion of fish in the upper channels were significantly greater during the residency period than during the emigration period (Table 2; $z_{\text{time}}=17.0$, $P<0.05$; $z_{\text{fish}}=4.2$, $P<0.05$). Use of the lower channels was greatest during the emigration period, both in terms of proportions of time spent in these habitats and the number of fish detected (Table 2; $z_{\text{time}}=14.6$, $P<0.05$; $z_{\text{fish}}=2.6$, $P<0.05$). Most fish (85%) detected in the lower channels occupied the upper channels for a mean of 132 ± 14 days before they were detected in the lower channels. Fish detected in both the upper and lower channels had a later mean emigration date (15 November 2007) than that of fish that did not use the lower channels (24 August 2007).

Only 4% (2 individuals) of Summer Flounder briefly occupied the tidal flat between October and December 2007 (6 ± 5 days, range: 1–11 days). Summer Flounder did not appear to regularly occupy the additional portions of the Wachapreague system monitored by the supplementary receivers. Only 7% (3 individuals) of Summer Flounder were detected by these receivers, and the mean residency was 6 ± 4 days (range: 0.2–13 days). Fish presence was, however, likely underestimated because of the limited coverage and the shorter period of receiver deployment.

Although the inlet region was frequented by Summer Flounder over the course of our study (Fig. 6B), fish spent a smaller proportion of time at the inlet (2%) than in the upper and lower channels (97%; Table 1). The mean time at the inlet was 2 ± 0.6 days. Not surprisingly, both the proportions of time and fish at the inlet were greatest during the emigration period (Table 2; $z_{\text{time}}=4.9$, $P<0.05$; $z_{\text{fish}}=3.0$, $P<0.05$).

Only 5 Summer Flounder in the upper channels moved between adjacent or nonadjacent receivers more than 10 times during the residency period. The mean observed activity did not vary significantly by week ($\chi^2=19.06$, $P=0.33$), but it did vary significantly with time of day; the mean activity index was significantly greater during night than during day ($\chi^2=6.13$, $P<0.05$). Individuals appeared most active during the flood tide or during the slack tide before ebb, but differences in mean activity among tidal stages were not statistically significant ($\chi^2=6.97$, $P=0.07$). Activity also was not affected

by differences in mean temperature for a given tidal stage ($\chi^2=0.46$, $P=0.55$).

Discussion

Migratory behaviors

The observed timing of Summer Flounder dispersal from the Wachapreague system (October through January) is consistent with the established seasonal progression of spawning migration from north to south (Smith, 1973; Morse, 1981; Kraus and Musick, 2001; Sackett et al., 2007). It most closely matches the reported timing of emigration for Summer Flounder in the nearby Chesapeake Bay. Summer Flounder primarily emigrate from Chesapeake Bay from October through December, and some fish emigrate as late as February (Desfosse, 1995; Henderson, 2012). In New Jersey's Mullica River–Great Bay estuary (~250 km to the north), acoustically tagged fish generally emigrated earlier—between August and December (Able et al., 1990; Roundtree and Able, 1992b; Szedlmayer and Able, 1993). By mid-September, 75% of tagged Summer Flounder had dispersed from a study site on the inner shelf near New Jersey (Fabrizio et al.³). In contrast,

³ Fabrizio, M. C., J. P. Pessutti, J. P. Manderson, A. F. Drohan, and B. A. Phelan. 2005. Use of the historic area remediation site by black sea bass and summer flounder. Northeast Fish. Sci. Cent. Ref. Doc. 05-06, 95 p.

75% of tagged fish in the Wachapreague lagoon system did not disperse until early December, and mean residence time was 1.5 times longer (130 days, June–January) than the time previously reported for the Mullica River–Great Bay estuary (86 days, May–December; Sackett et al., 2008). Seasonal changes in temperature strongly influenced residence time, as indicated by the increase in dispersal rates with the seasonal decline in temperature. A similar relationship between water temperature and seasonal migration was observed in winter flounder through the use of passive acoustic telemetry (DeCelles and Cadrin, 2010).

On the basis of the life history of Summer Flounder, fish that dispersed from the Wachapreague lagoon system during the emigration period (after 11 October 2007) were most likely moving offshore to spawn. Our study revealed that smaller fish were more likely than larger fish to leave during the emigration period, confirming previous reports that larger Summer Flounder commence spawning migrations earlier than smaller fish (Smith, 1973). Summer Flounder that dispersed from the Wachapreague system during the emigration period had significantly greater odds of returning to the system the following year than did those fish that dispersed during the residency period.

The percentage of fish returning to the Wachapreague lagoon system (36%) was similar to the percentage reported for more northern estuaries (25–35% and 39% in New York and New Jersey, respectively; Poole, 1962; Sackett et al., 2007). Unlike returns in a previous mark-recapture study (Desfosse, 1995), returns to the Wachapreague lagoon system were not detected after April, although the expected battery life of our transmitters would have permitted detection through July 2008. Summer Flounder did return to the Wachapreague lagoon system as early as February, indicating that some fish may actually remain in this system for upwards of 10 months (i.e., from February to the following December).

Acoustic telemetry permitted the identification of early and temporary emigrants from estuaries in this and a previous study (Sackett et al., 2007). It is possible that early emigrants migrate to the outer continental shelf to spawn, but the timing of these events is much earlier (typically in the early summer) than the timing reported for the spawning migration of this species. Fish that disperse early or temporarily may instead occupy habitats on the inner continental shelf or in other estuaries before final emigration to the outer continental shelf to spawn. On the basis of the confirmed observation of a single fish that was subsequently detected in Delaware Bay approximately 2

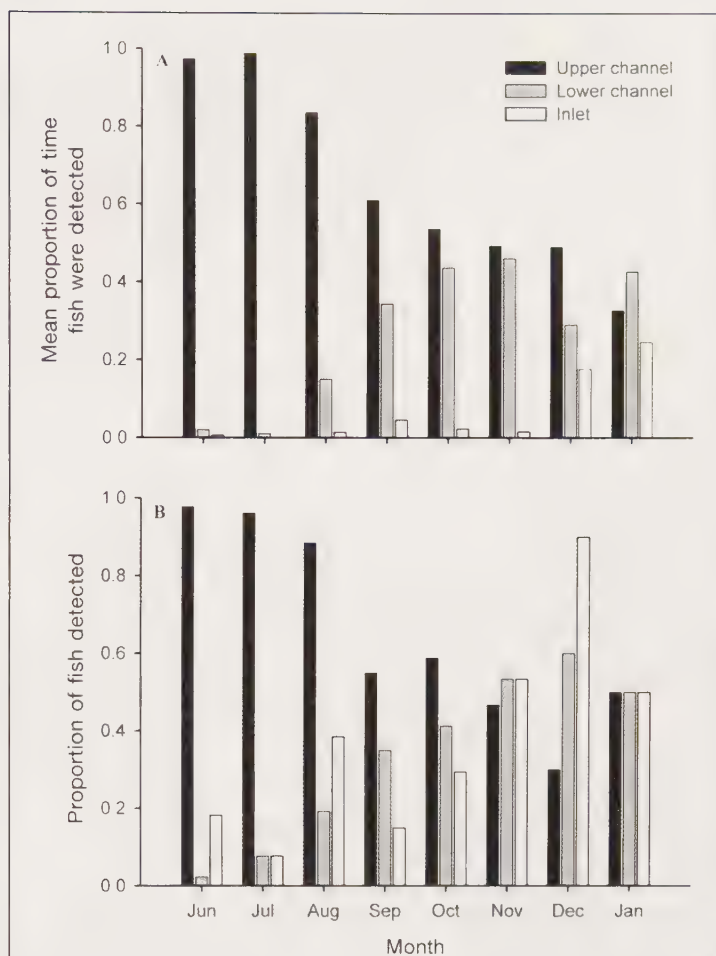


Figure 6

(A) The monthly mean proportion of time that Summer Flounder (*Paralichthys dentatus*) occupied the upper channels, lower channels, and Wachapreague Inlet in the Wachapreague lagoon system from June 2007 to January 2008. For a given month, the proportion of time that individual fish occupied each region was calculated as the ratio of the amount of time that a fish resided in a region in relation to the total time it was detected that month, with proportions for a month adding to 1. (B) The monthly proportion of individual Summer Flounder detected in the upper channels, lower channels, and Wachapreague Inlet. The proportion of fish that occupied a region was determined as the ratio of the number of individual fish identified in that region to the number of fish detected in the system that month. The sum of the proportions of fish in each region could be <1 if not all fish could be assigned objectively to a region in any given month. The sum of the proportions of fish that used each region could be >1 if a single fish occupied more than 1 region in any given month.

weeks after tagging, there is at least some movement of Summer Flounder between coastal estuarine systems within the same summer. Previous mark-recapture studies have also indicated that Summer Flounder move from Virginia to more northern MAB estuaries

Table 2

Mean proportions of time Summer Flounder (*Paralichthys dentatus*) spent in each region of the Wachapreague lagoon system (upper channels, lower channels, and inlet) by month and period (residency and emigration); proportions of Summer Flounder found in each area by month and period; and numbers of fish present in the system (*N*) by month and period. The residency period was from 8 June to 10 October 2007, and the emigration period was from 11 October 2007 to 17 January 2008. Activity in tidal flats and supplementary channels was not included because of the low numbers of detections in these areas.

		Mean proportion of time (%)				Proportion of fish (%)		
		<i>N</i>	Upper channels	Lower channels	Inlet	Upper channels	Lower channels	Inlet
Month								
2007	June	45	97.3	2.0	0.6	95.6	2.3	17.8
	July	31	98.9	1.1	0.1	80.7	6.5	6.5
	August	30	83.6	15.0	1.4	74.2	16.1	32.3
	September	25	61.1	34.4	4.6	44.0	28.0	12.0
	October	23	53.7	43.7	2.3	43.5	30.4	21.7
	November	16	49.4	46.1	1.6	43.8	50.0	50.0
	December	10	49.0	29.1	17.7	30.0	60.0	90.0
2008	January	2	32.7	42.7	24.6	50.0	50.0	50.0
Period								
	Residency	45	86.3	11.5	1.5	97.8	17.8	40.0
	Emigration	16	48.9	14.6	5.6	50.0	56.3	87.5

(Lucy and Gillingham⁴), although not within the same year (as observed in our study). Early or temporary emigration from estuaries may occur in response to environmental cues not monitored in this study, such as barometric pressure or rainfall, or may simply reflect variation in migratory behavior among fish (Sackett et al., 2007; Henderson, 2012). Future research is needed to investigate the drivers of early and temporary emigration and the destination of fish that engage in these behaviors.

Within-estuary behaviors

The distribution of Summer Flounder in the Wachapreague lagoon system was comparable to that observed in the Mullica River–Great Bay estuary (Sackett et al., 2008); in both studies, adult Summer Flounder were primarily detected in the lower bay near the inlet. In our 1-year study, nearly all tagged fish were released in the upper channels (where most fish remained). It is possible that tagged fish released in other regions exhibit fidelity to those regions and that the distribution of tagged Summer Flounder within the system differs by year; however, little difference was observed for Summer Flounder in the region of primary detection

over the 2-year study in the Mullica River–Great Bay estuary (Sackett et al., 2008).

Although adult Summer Flounder occupy a variety of habitats in estuaries, sandier substrates enable these flatfish to bury themselves easily (Bigelow and Schroeder, 1953; Dahlberg, 1972; Orth and Heck, 1980; Roundtree and Able, 1992a). These substrates are often found in areas with high-velocity currents, such as those currents in channels near an inlet. Fishes and crustaceans compose a large portion of the adult Summer Flounder diet (Latour et al., 2008; Buchheister and Latour, 2011), and higher current velocities most likely deliver more potential prey into an area per unit of time. Summer Flounder have been observed in deeper areas (~8.5 m) of other MAB estuaries, presumably because of stable environmental conditions (Smith and Daiber, 1977; Sackett et al., 2008). For future acoustic telemetry studies in the Wachapreague lagoon system and in other estuaries, the effects of release location and year on tagged fish should be considered in order to make inferences about Summer Flounder distribution and habitat preferences within estuaries.

The coexistence of behavioral types has been noted in other species and postulated to result in approximately equal fitness among individuals (Bolnick et al., 2003; Kobler et al., 2009). Summer flounder appear to fit this pattern. In our study, the majority of Summer Flounder resided primarily in the upper channels, although a small group of fish (12 individuals) did use the lower channels. The use of the lower channels increased as the study period progressed, and these fish

⁴ Lucy, J. A., and L. Gillingham. 2009. Virginia Game Fish Tagging Program annual report 2008. VIMS Marine Resource Report No. 2009-4. Virginia Sea Grant Publication No. VSG-09-03, 149 p. [Available from <http://web.vims.edu/library/GreyLit/VIMS/mrr09-04.pdf>.]

had a later mean dispersal date than the fish that did not use the lower channels. Divergent patterns of behavior have been observed in other acoustic telemetry studies on Summer Flounder. In the Mullica River–Great Bay estuary, up to 80% of fish remained in the lower bay near the inlet where they were tagged (Sackett et al. 2008), but several fish did move into the river system. At an artificial reef in the Chesapeake Bay, larger Summer Flounder were more likely to stay in close proximity to the reef structure than were smaller fish (Henderson, 2012).

The behavior of Summer Flounder in estuaries has been described as sedentary with only minor activity before fall emigration (Desfosse, 1995; Sackett et al., 2008; Henderson, 2012). This description characterized Summer Flounder in the Wachapreague lagoon system, where fish rarely exhibited large-scale movements (100s of meters) between receivers in the upper channels. However, passive telemetry cannot capture small-scale movements adequately, and fish may have been active within smaller areas (<100s of meters). Active tracking of Summer Flounder in the Mullica River–Great Bay estuary revealed that fish were in motion within small areas (0.18 km²) for most of the time that they were observed and that small-scale movements in deeper waters (~8.5 m) were not related to tidal currents or temperature (Sackett et al., 2008). Small-scale activity was attributed to feeding, competition, or territorial behaviors (Sackett et al., 2008). We did not observe significant effects of temperature or tidal stage on large-scale (100s of meters) fish activity in the upper channels during the residency period. Fish in these regions may have an ample supply of prey delivered by the currents and, therefore, may not need to make large-scale movements or use energetically beneficial tidal conditions (e.g., Wirjoatmodjo and Pitcher, 1984; Szedlmayer and Able, 1993; Miller, 2010).

During the residency period, fish activity in the upper channels of the Wachapreague lagoon system was significantly greater at night than during the day. Laboratory-based observations revealed that Summer Flounder are more active during the day (Olla et al., 1972), but such studies considered activity on a much smaller scale (e.g., in a seawater tank that was 10.6×4.5×3.0 m). Similar large-scale (200–400 m) activity of Summer Flounder in the Chesapeake Bay also was greatest at night and influenced by lunar phase (Henderson, 2012). Although benthic foragers (such as Summer Flounder) are generally more light sensitive than are other estuarine pelagic piscivores (Horodysky et al., 2010), the foraging ability of visual predators is most likely limited at night. Therefore, night-time movements may be associated with behaviors other than prey localization and feeding.

Conclusions

One of the benefits of acoustic telemetry is the ability to identify variation in behavior within a population that renders a species differentially vulnerable to estuarine conditions, predation, and harvesting. Differences and similarities in behavior patterns observed for a species by multiple researchers can be used to identify factors that influence such patterns. Our study confirms that, although the life history and migration dynamics of Summer Flounder are well described, individual fish are not uniform in their use of estuaries during summer residencies throughout the MAB.

Residence times vary by estuary, indicating that local conditions are important to population success. Fish size may also effect how long Summer Flounder remain in an estuarine system. As was found in a northern MAB estuary, most tagged Summer Flounder in the Wachapreague lagoon system were sedentary over 100s of meters and remained in deeper (>3 m) waters near the inlet until they undertook the spawning migration (although a small number of individuals did make use of other regions).

Further research is needed to consider the effects of release location and year on distribution of tagged Summer Flounder. Studies that combine acoustic monitoring with the distribution and availability of predators and prey may help explain observed distributions. Establishment of a network of strategic acoustic monitoring stations within multiple MAB estuaries and along the continental shelf would enable monitoring of fish in these habitats and could help clarify the fate of early or temporary emigrants (Grothues et al., 2005; Able and Grothues, 2007). A better understanding of Summer Flounder habitat preferences and behaviors in estuaries along their range of distribution is essential for protecting areas that promote year-class strength and spawning success.

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Title page should include authors' full names and mailing addresses and the senior author's telephone, fax number, and e-mail address. **Abstract** should be limited to 250 words (one-half typed page), state the main scope of the research, and emphasize the authors' conclusions and relevant findings. Do not review the methods of the study or list the contents of the paper. Because abstracts are circulated by abstracting agencies, it is important that they represent the research clearly and concisely.

General text must be typed in 12-point Times New Roman font throughout. A brief introduction should convey the broad significance of the paper; the remainder of the paper should be divided into the following sections: **Materials and methods**, **Results**, **Discussion**, **Conclusions**, and **Acknowledgments**. Headings within each section must be short, reflect a logical sequence, and follow the rules of subdivision (i.e., there can be no subdivision without at least two subheadings). The entire text should be intelligible to interdisciplinary readers; therefore, all acronyms, abbreviations, and technical terms should be written out in full the first time they are mentioned.

For general style, follow the U.S. *Government Printing Office Style Manual* (2008) [available at <http://www.gpoaccess.gov/stylemanual/index.html>] and *Scientific Style and Format: the CSE Manual for Authors, Editors, and Publishers* (2006, 7th ed.) published by the Council of Science Editors. For scientific nomenclature,

use the current edition of the American Fisheries Society's *Common and Scientific Names of Fishes from the United States, Canada, and Mexico* and its companion volumes (*Decapod Crustaceans*, *Mollusks*, *Cnidaria and Ctenophora*, and *World Fishes Important to North Americans*). For species not found in the above mentioned AFS publications and for more recent changes in nomenclature, use the Integrated Taxonomic Information System (ITIS) (available at <http://itis.gov/>), or, secondarily, the California Academy of Sciences *Catalog of Fishes* (available at <http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>) for species names not included in ITIS. Citations must be given of taxonomic references used for the identification of specimens. For example, "Fishes were identified by using Collette and Klein-MacPhee (2002); sponges were identified by using Stone et al. (2011)."

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Word usage and grammar that may be useful are the following:

Aging For our journal the word *aging* is used to mean both age determination and the aging process (senescence). The author should make clear which meaning is intended where ambiguity may arise.

Fish and fishes For papers on taxonomy and biodiversity, the plural of *fish* is *fishes*, by convention. In all other instances, the plural is *fish*.

Examples: The fishes of Puget Sound [biodiversity is indicated];

The number of fish caught that season [no emphasis on biodiversity];

The fish were caught in trawl nets [no emphasis on biodiversity].

The same logic applies to the use of the words *crab* and *crabs*, *squid* and *squids*, etc.

Sex For the meaning of male and female, use the word *sex*, not *gender*.

Participles As adjectives, participles must modify a specific noun or pronoun and make sense with that noun or pronoun.

Incorrect: *Using the recruitment model, estimates of age-1 recruitment were determined.* [Estimates did not use the recruitment model.]

Correct: *Using the recruitment model, we determined age-1 estimates of recruitment.* [The participle now modifies the word *we*, those who were using the model.]

Incorrect: *Based on the collected data, we concluded that the mortality rate for these fish had increased.* [We were not based on the collected data.]

Correct: *We concluded on the basis of the collected data that the mortality rate for these fish had increased.* [Eliminate the participle and replace it with an adverbial phrase.]

Equations and mathematical symbols should be set from a standard mathematical program (MathType) or tool (Equation Editor in MS Word). LaTeX is acceptable for more advanced computations. For mathematical symbols in the general text (α , χ^2 , π , $\pm$, etc.), use the symbols provided by the MS Word program and italicize all variables. Do not use photo mode when creating these symbols in the general text.

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